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Erratum

Page 287, foot note No. 11, for "mymecophilous" read "myrmecophilous."

Tropical plant pathology and mycology[1]

F. L. Stevens

My subject divides into two practically distinct topics. As regards both I shall limit myself to first-hand knowledge, to what I have myself seen in tropical countries including all of the American tropics, Hawaii and the Philippines, omitting, therefore, from consideration Africa and Asia. I shall also take the liberty of referring to occasional subtropical regions.

First, I shall speak regarding plant pathology of cultivated plants. Diseases, as you will surmise, are both more numerous and more destructive than in temperate regions due usually to continuous growth of the host and parasite, without the interruption of a hibernation period. So rapid is fungous growth that logs of large fallen trees do not for long cumber the ground in the jungle since they decay so rapidly. It is not unusual to see an automobile of recent make with a punk of a *Polyporus* several inches across growing out from the top. In buying second-hand cars the first item to look for is freedom of wood parts from fungous invasion. In clearing land for banana planting the trees are merely felled, leaving fungi to do the rest. Similarly host growth is so rapid that a clearing reverts to luxuriant jungle growth within a few years.

There is no great difference in kind between tropical and temperate diseases. The wilts, bacterial and fusarial, are there, as are the mildews, smuts, rusts anthracnoses and diseases caused by *Rhizoctonia*, *Sclerotium Rolfsii*, *Pythium*, *Phytophthora*, etc., but all in greater abundance and destructiveness than here. Also there are, of course, numerous genera and species of parasites not known in temperate regions; particularly abundant are the entomogenous fungi and the algae.

It may be well to mention a few very destructive diseases, though perhaps all are known to many of you.

The fusarial banana wilt claims many square miles of territory and is so destructive that miles of railroad have been seriously handicapped through lack of shipping so that perhaps only two or three trains a week now run where formerly there were as many each day.

The coffee rust due to *Hemileia* has devastated large areas. We may well be thankful that prompt action in the Porto Rican Experiment Sta-

tion nullified its only entrance in this hemisphere. The cacao witches' broom has spread in such exceeding destructiveness that Ecuador, once the foremost producer of the chocolate bean, is now forced largely to abandon this crop. The coconut bud-rot has circled the world, the bud-rot naturally killing the trees. On sugar cane are numerous destructive fungous diseases and many of the virus type. On rice are listed more than thirty fungi; on *Bambusa spinosa*, fifty. Rubber plants are much beset and seriously.

In general these destructive diseases have received adequate study only in the cases of those crops supported by large corporate interests. The banana disease has been thoroughly studied, due to the interests of the United Fruit Company; sugar cane by the extremely fine Experiment Station supported by the Hawaiian sugar planters; similarly the pineapple diseases by the Hawaiian pineapple growers. The extensive rubber interests look after the diseases of rubber.

Aside from researches supported privately by such large money interests, comparatively few extensive researches have been carried out. Exceptions, of course, can be mentioned, as that of the remarkably fine research of Stahel proving that *Marasmius* is the cause of the cacao witches' broom.

The lesser of the major and most of the minor crops have received but little attention. Due to diversity of crops and multitude of diseases the task is enormous, far beyond the facilities and workers available. Thus it is that in one respect, with no reflections upon the workers there, the tropics, as regards knowledge of plant pathology, are now in the main in pioneer days, much as it was in the United States when Lamson-Scribner and Halsted in 1888 were writing descriptions of diseases now widely known. In many regions in the tropics it is now possible to step out, find and describe many crop diseases that have not as yet even been listed. Thus the tropics offer a field of delight to the pathologist.

Treatment for disease in the tropics offers especial difficulties due to rapid growth and often excessive rain; these difficulties, however, are partially compensated by very cheap labor. Adequate treatment is, however, practically limited to those cases where a large corporate interest is concerned. In general, spraying by the small planter or spraying of minor crops, such as pechi, papaya, taro, fig, luffa, betel, breadfruit, nutmeg, cassava, etc., is unknown. The only exception that occurs to me is in the case of grapes in certain grape sections in South America.

Mycologically, the tropics are, of course, wonderfully rich in forms and are comparatively but little known. The Philippines may be cited as an example of lack of any completness in collecting. A map compiled by Dr. Merrill shows the Philippine regions that have been well and thoroughly

collected at all seasons, those less collected, and those not collected at all. This refers in the main to collecting of vascular plants with comparatively little attention given to the fungi. The showing would be much poorer in many tropical countries—for example, the vast regions of tropical America, particularly the great Amazon valley and its adjacent mountains.

The vast numbers of species in such regions may be imagined when one realizes that Mt. Maquiling near Manila, a mountain some 3,700 ft. high and about five miles in basal diameter, is said by Dr. Merrill to bear about twice as many species of woody plants as the whole United States, perhaps with Canada included. The non-woody plants, of course, abound equally. This same profusion of species occurs on most Philippine mountains and usually with a flora markedly differing from mountain to mountain.

This profusion of hosts indicates a similar profusion of parasites. There are more than 40 species of *Ficus* recorded in the Philippines each with several parasites all its own; yet there are 107 additional species of *Ficus* known from the islands from which the parasitic fungi have not been recorded. Extend this line of thought of abundance of species and almost absence of any adequate collection to include all of the tropical regions and it will readily be seen that Saccardo's 24 volumes of the "Sylloge Fungorum" would needs be doubled or trebled to contain the fungi of the tropics.

A few remarks may be appropriate as to some of the most common groups of tropical fungi.

The powdery mildews abound in the tropics, but so far as my experience has shown they are never ascigerous. The Meliolas and their kin, eight closely related genera, have from first knowledge of them been likened to the powdery mildews due to their superficial mycelium, and perithecia often with appendages strikingly resembling these of the powdery mildews. They are characteristically tropical since only five species are known from Europe, fifteen from the United States, while 158 are recorded in the Philippines alone. Nearly 1,000 species have been recorded and many times that number remain to be recorded. The two forms of hyphopodia, the capitate and mucronate, are organs of unknown function, though that of the former is probably to serve as a hold-fast and to bear haustoria. Often these fungi are heavily parasitized by various and numerous Hyphomycetes and other fungi. These parasites were formerly erroneously regarded as conidial forms of the Meliolas. These numerous parasites are of world distribution on Meliolas, thus betokening long association with them. The Meliolineae have no conidia, thus presenting strong contrasts with the powdery mildews. The Meliolas are highly specialized as to their hosts and there is evidence that modifications have occurred upon given

osts. It thus frequently happens that several distinct, but evidently related forms are found upon one host species. The evolution of these species has occurred during the tenancy of this phylum upon this host. On the Convolvulaceae is a group of species characterized by its globose hyphopodia. On Leguminosae are many species characterized by variously toothed setal tips. On palms are 10 species with the setal tips that are much toothed.

Such evolution as has occurred, giving us the groups of related species that we now recognize, may have occurred on the given hosts or with them. Thus a primitive form may have lived ages ago on a primitive host form in, for example, the Leguminosae. As the primitive host differentiated to give us the various genera and species that have arisen from it, the *Meliola* residing upon it presumably also at the same time became differentiated; or on the other hand the *Meliola* may have differentiated without any accompanying changes in the host. There is evidence in Hawaiian material that an *Amazonia* and an *Actinodothis* which now show quite distinctive characters have evolved from a common *Meliola* ancestor since it originally adopted *Perrottetia* as a host.

The Meliolineae with their magnificent aggregate of species offer a delightful field for phylogenetic study. It appears at present that the primitive stock from which this group arose was non-hyphopodiate with 8-spored persistent asci with variable spore septation, and that this stock diverged along two lines, one with 3-septate spores, the other with 4-septate spores. The Microthyriaceae comprise what is probably the largest family of tropical fungi and occur in enormous numbers of genera and species. They are very beautiful with their radiate perithecium and delicate, usually hyphopodiate, mycelium and certainly suggest relationship to the Meliolas, to which group bridging genera occur. Further study here should add much to phylogeny. Many of the temperate zone Hysteriales, as recorded, possess a radiate structure strongly reminiscent of the Microthyriaceae, though none known to me show the hyphopodia so characteristic of the Microthyriaceae. It is quite possible that some fungi recorded as Hysteriales belong to the Microthyriaceae. Much morphological study is here needed. No obvious transition forms between the Erysiphaceae and the groups above mentioned are known, but may yet be found. The Dothideales are bridged to the Meliolineae by several forms such as *Actinodothis* and *Amazonia*, but this may apply only to a section of the Dothideales which are probably of polyphyletic origin. The Trichopeltaceae is a family of the Hemisphaeriales of quite unique characters since the plant body typically consists of a layer of laterally adhering cells. The plant body is strap-shaped and one cell thick, strikingly resembling in structure one of

the liverworts. Though abundant in the tropics they have been but little collected or written of. Some features of their growth are shown in the slides. The perithecia arise from the lower side of the thallus. In Hawaii I found some of these fungi that bore no perithecia, but were conidial.

A most interesting fungus from Hawaii which I collected only once, on *Rubus*, perhaps shows a bridging form between these fungi with the liverwort-like plant body and the ordinary filamentous fungi, since it possesses both forms of structures. The Trichothyriaceae parasitic on fungi, largely on the Meliolineae, suggest the family just discussed but their real affinity is uncertain. The Hemisphaeriaceae, or fly-speck fungi, almost or quite unknown here, are very common in the tropics. They are true to their fly-speck name in appearance and have been studied hardly at all except as to their most apparent morphology. They are very variable in ascus and spore characters and are highly specialized as to host relation.

The Sooty Moulds of course abound. Their great variability and many taxonomic tangles are well enough known to you through your few temperate species which for long were called Meliolas. It is needless to mention the great increase in these difficulties in the tropics.

The Myriangiales so rare here are quite abundant tropically.

The Dothidiales abound in a way unknown here, constituting probably one of the three largest orders of tropical fungi. Their taxonomic status, as admitted by Sydow, is far from satisfactory. They verge indistinguishably toward the Sphaeriales on one hand and to the Perisporiales and Hemisphaeriales on the other. Much morphologic study is needed to brace up taxonomy and phylogeny. The occurrence of more than 40 recorded species on the single genus *Ficus* suggests both their abundance and the need of biologic and morphologic studies.

Connecting forms between groups which may be of much phylogenetic interest occur frequently in tropical collections. The genus *Graphiola* long puzzled mycologists who knew not whether to class it as a smut, a rust, one of the Imperfecti or what not. The solution eventually was to erect the family Graphiolaceae. But did that help? In Panama I found a fungus which I christened *Shropshiria* which seems to me, I hope correctly, to be kin to *Graphiola*, though in many respects different from it. This finding leads to the hope that more kin may eventually be found and so suffice to finally lead to the placing of this floating group in connection with the rest of the fungi.

Practically none of the above mentioned groups has been studied cytologically, as to the origin of the asci, or as to biological specialization.

Rusts in the tropics are of great interest since so many apparently aecial forms prove on germination to be telial. Further study may reveal

chapters comparable to the interesting *Caeoma nitens* story of the temperate regions; indeed one such case was strongly suggested by my study of Philippine rusts. In case of the insular flora of Hawaii it is interesting to note that six of the rusts are apparently of American derivation while there is only one from the west. The paucity of indigenous smuts in Hawaii is peculiar and striking as compared with their greater abundance in Porto Rico.

In conclusion I would emphasize the wonderful richness of the tropics in all fields of mycology and pathology and urge the importance of collecting trips and of field study.

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A biological survey of the Maya area[1]

HARLEY HARRIS BARTLETT

The study of the wide-spread Maya civilization which once covered much of Central America and southern Mexico is a major interest of Tulane University, our host institution at this meeting. Its Department of Middle American Research under the leadership of Prof. Frans Blom, is unique among American universities. Research in Maya archeology has been carried on for twenty-five years by the Department of Historical Research of the Carnegie Institution of Washington. The Field Museum is active in the Maya field, and the Peabody Museum of Harvard University has been a pioneer with a record of research extending through more than half a century. The beginnings of Maya research were made by the American consul to Yucatan, Stephens, whose four intensely interesting volumes, published in 1841 and 1843, directed the attention of Maudslay, of England, to the Maya region, where his investigations were of monumental importance.

Maudslay has had worthy followers, and archeological data have accumulated rapidly. But Kidder of the Carnegie Institution now says that "proper utilization of these data . . . can be made only in the light of accurate information as to the biological nature of the populations concerned, and as to the environment in which they lived. . . . It has accordingly been necessary to call for aid by workers in several non-archeological fields. Furthermore, the principle that in any investigation one should proceed from the known to the unknown, which in archeology means that one should work from the known present to the unknown past, has induced analysis of modern conditions and post-conquest history."

The analysis of modern conditions has been undertaken through collaboration of the Carnegie Institution with several institutions. The School of Tropical Medicine of Harvard University has undertaken a medical survey. The University of Chicago has assigned Dr. Redfield and Dr. Andrade to the fields of Maya ethnology and linguistics, respectively. Geological work has been started by C. Wythe Cook of the U. S. Geological Survey. The University of Michigan has committed itself to a twenty-year program of biological survey, and has completed the work of one field season.

[1] Based on an invitation address presented in a symposium on Tropical Botany before the joint session of Section G (Botanical Sciences) of the American Association for the Advancement of Science, the Botanical Society of America, the American Phytopathological Society, and the American Society of Plant Physiologists at New Orleans, 29 December, 1931.

Of course no one believes that a biological survey carried on by one institution will give complete and definitive information in twenty years. Nevertheless, if the work is well balanced it ought to establish the main outlines of plant and animal geography, to determine the main ecological phenomena accompanying man's occupation and abandonment of agricultural land, and to work out the ethnobotany and economic botany of the region in considerable detail.

The Maya area includes all of the Yucatan peninsula and considerable adjoining parts of Central America and Mexico. If defined broadly, it covers part or all of the following political units: Guatemala, Salvador, British Honduras, Honduras, Yucatan, Quintana Roo, Campeche, Tabasco, Chiapas, Oaxaca, Vera Cruz, and Tamaulipas. From a biological standpoint this is a region of much diversity, but there is a certain unity about it as well. It includes a representative part of the Atlantic *tierra caliente*, the only part of Mexico and Central America in which the flora has a large West Indian element. The considerable amount of endemism in the Yucatan peninsula increases the interest of the Maya area as a phytogeographic unit.

This paper need hardly touch upon the earlier biological history of the region since it was covered by Hemsley in Godman and Salvin's "Biologia Centrali-Americana." Furthermore, since this is a botanical audience and the speaker is a botanist, in what follows I shall confine myself to the history of botanical exploration and to the statement of what botanists are now doing. The more general title of the paper was chosen in order to emphasize the fact that the predominant part of the Michigan project is zoological, and is being carried out under the general supervision of Mr. F. M. Gaige, Director of the Museum of Zoology.

It goes without saying that on the botanical side much more has been accomplished in the past than we can hope to add during our twenty-year program. In order to utilize accumulated data to the best advantage, however, much new work must be done in the way of correlation and integration. Descriptive science ordinarily grows in a chaotic and haphazard fashion, but it does grow even without much directive thought. With one institution planning to fill the neglected gaps, and to supplement the work of other institutions, a twenty-year program ought to accomplish very valuable results.

Hemsley's great work serves us the more conveniently as a point of departure because of the facts that prior to its publication (1879–1888) there had been relatively little participation from the United States in the botanical exploration of the region, and that most of the materials available in this country have been accumulated subsequently.

As a matter of fact, the data brought together by Hemsley were so deficient for the Maya area that they served chiefly to indicate the extent to which it had been neglected. For British Honduras, Hemsley was able to record, aside from scattered specimens, only a single collection of as many as forty species. He cited only 152 species from the whole of Honduras. American participation in floristic investigation of the Maya area has been so continuous since the publication of Hemsley's work that our four major botanical institutions offer greater resources to the investigator than are to be found in Europe.

Among more recent collectors the first to be mentioned should be Sereno Watson of the Gray Herbarium. His interest in Guatemala was whetted by a lack of information so great that his friend Walter T. Brigham, an observant and critical traveler, wrote, "Any botanist who would devote three months to the thorough exploration of the valley forests of Guatemala ought to add not less than a hundred new species to the flora of the region and also determine the species of most of the beautiful cabinet woods now known only by their native names." During two months in the winter of 1886 Watson collected in the Department of Izabal five hundred species of plants, including many new species, the first extensive Central American collection to become part of an American herbarium.

From 1890 to 1907 Captain John Donnell Smith of Baltimore took Guatemala and adjoining regions as his special field of interest, engaging personally in field work from 1890 to 1896 and later cooperating with other botanists, whose expeditions he financed and whose collections he studied and distributed. In 1907 he published the eighth and last part of an enumeration of the plants of Guatemala (including as well many records from the other Central American republics) in which he cited 3736 species, of which 1189 were not listed by Hemsley. Captain Smith bequeathed his collections to the Smithsonian Institution. Baron von Tuerckheim, whose earlier collections, at Kew, were made as far back as 1878, was Captain Smith's chief collaborator.

Before the end of Captain Smith's activity other Americans were beginning to take an interest in Guatemala. The "Peripatetic School of Botany" of Prof. W. A. Kellerman came to an unfortunate end. His death from malaria in Guatemala in 1908 closed a project of botanical exploration which he had hoped to carry on with the aid of students as a supplement to the instruction in his department at Ohio State University. Mr. C. C. Deam, before he became State Forester of Indiana, made botanical expeditions to Guatemala, in 1905 and 1907, which added much to our knowledge of the flora. One of the most curious of all Cactaceae, the genus *Deamia* of Britton and Rose, commemorates his activity in Central

America. The most complete set of his tropical plants is at the University of Michigan.

From a monographic, as opposed to a floristic or economic standpoint, the most outstanding American work has been that of Dr. A. S. Hitchcock, whose collections of grasses in 1911 from all parts of Central America except British Honduras, supplemented by those of previous botanists, provided the material for his "Grasses of Central America."

The only lower cryptogams which have had at all intensive study are the rusts. For many years E. W. D. Holway devoted himself to the study of tropical rusts, including those of Guatemala. He died in 1923, leaving his herbarium to the University of Minnesota. It has fallen to the lot of few modern amateur botanists to make as indelible a record in his chosen field as he did. His rusts were generally collected in districts where no previous work had been done, and of course a good many of the species proved to be new to science.

Just as the work of Hitchcock on grasses and of Holway on rusts represents the beginning of intensive efforts to complete our knowledge of particular families over large ranges, so the other type of systematic attack, in which every plant possible in a small restricted area is accounted for, has also just begun in the Maya area. It is to the credit of Standley that he has produced the first local floras for our region, one of which, the "Flora of the Lancetilla Valley, Honduras," stands alone from the standpoint of its adequacy for a restricted area. Nothing of moment preceded it for Honduras except the scanty records in Hemsley's "Biologia" and John Donnell Smith's "Enumeratio," and the collections of Percy Wilson, made for the New York Botanical Garden in 1903. Standley spent several months in the field in 1927–28 and collected over 3000 numbers in all groups of plants, mostly within a very restricted area about Tela. His flora, therefore, will be especially valuable for florestic comparisons when other localities shall have been studied in equal detail. Of course not many places are likely to receive the detailed attention that Standley has devoted to the Lancetilla Valley, and it is hoped that the latter may come to be considered as a classic locality for which future records will be published as they accumulate.

The first good collection from British Honduras to reach this country was made from 1905 to 1907 by M. E. Peck for the Gray Herbarium. It consisted of over 900 numbers and contained a considerable number of new and interesting plants of which there has been only a scattered record. The grasses, which have been made the subject of a paper by F. Tracy Hubbard, were sufficiently well represented to enable Hubbard to draw the interesting conclusion, concurred in by Dr. Robinson, who has

studied other families, that the flora of British Honduras is composed of some Mexican but chiefly of West Indian and South American elements.

British Honduras had its political origin in the early struggles of the English and Spanish for control of the formerly valuable logwood trade. With the eventual decline of logwood as an article of commerce, mahogany rose to first place as an export, and then chicle gum became very important for a time, but, through all the vicissitudes of commerce, uncultivated products of the forest have always been the mainstay of the colony. The "bush" was long looked upon as an inexhaustible mine, but a survey of the remaining mahogany, completed about 1922, showed the necessity of a constructive forestry policy for the future. A Forest Department was inaugurated to which the colony has been so hostile that its effectiveness has lately been greatly reduced. Stimulated by Professor Record of Yale University, and with the help of Standley in the determination of the material, several members of the Forest Department have considerably extended our knowledge of the composition of the complex rain forest. Especially valuable have been the lists of scientifically identified local names which Record has issued, in the pages of "Tropical Woods." The Forest Department is making detailed maps showing the distribution of forest types over the colony. These maps have not yet been published but are available for consultation.

The recent work of three collectors has been especially important in British Honduras. C. L. Lundell has worked in the Orange Walk District, and his large collections of 1929 supplied the first adequate representation of the flora of any limited region of the colony. A small collection by J. S. Karling in 1928 was remarkably productive of new species and extensions of range. The greatest additions, however, have come through an independent collector, Mr. William A. Schipp, from whose astonishingly rich collections Dr. Standley has described many novelties.

We may now turn from the strictly Central American part of the Maya area to that part which lies in Mexico.

While the "Biologia Centrali-Americana" was going through the press, an American physician, George F. Gaumer, began the work upon which our knowledge of the flora of Yucatan is almost wholly based. His first specimens, collected in 1885–86 on Cozumel Island, were listed in an appendix to Hemsley's fourth volume. The Field Museum was founded in 1893, and the curator of its herbarium, the late Dr. Charles F. Millspaugh, collected in Yucatan in 1894. He became acquainted with Dr. Gaumer, who collaborated with the Field Museum until about 1921. The first set of Gaumer's plants, aggregating more than 5400 specimens, is in the Field Museum. Dr. Millspaugh again visited Yucatan in 1899. Other

collectors in Yucatan have been Profirio Valdez (1887–1896), Witmer Stone of the Philadelphia Academy (300 plants, 1890), E. A. Goldman of the U. S. Biological Survey (1901), the archelogists Eduard and Cecilia Seler (several hundred species, 1902–1911), J. M. Greenman (180 species, 1906), G. N. Collins (1912–13), Dr. J. B. Becquaert (100 species, 1929). The Field Museum has been fortunate in securing sets of most of these collections and the most important older collection (that of Arthur Schott, 850 plants, 1864–66) as well, so that its holdings of over 7000 sheets represent the most important source of knowledge of the Yucatan flora. The utilization of this material was begun by Millspaugh, and brought to a conclusion after a laspse of 30 years in Standley's "Flora of Yucatan," issued in 1930. Dr. Gaumer recorded a great number of Maya plant names and uses. These, compiled by Standley from Gaumer's manuscript and specimen labels, constitute an important and valuable body of data for the correlation of the botany and ethnology of the region. In this field Gaumer has been followed by Ralph L. Roys whose "Ethnobotany of the Maya" has just appeared.

The work of Mr. Roys is the second volume of the publications of the Middle American Research Series of Tulane University. He has brought together manuscript materials and local publications dealing with medicine, arranged them according to a logical system, and published both the Maya text and his translation. Yucatan is the only part of America where, after the Spanish conquest, the Indians themselves wrote a considerable body of medical literature in their own language but in European script. Although none of the existing manuscripts is older than the 18th century, there is every probability that they were passed from hand to hand and copied, so that the literary materials are older than the actual manuscripts. They contain much that is European in origin, but it is thinly superposed upon a substratum of native lore which can readily be distinguished. Mr. Roys' study will be of basic importance. It doubtless includes the vernacular names of most of the important medicinal plants in Yucatan, and presents a challange to the botanist to trace the identity of the unknown plants as well as to confirm the determinations which have already been made. He and Tulane University are to be congratulated upon its timely publication.

Standley's "Flora of Yucatan" covers not only the political state of Yucatan, but also what little is known of adjacent areas (except British Honduras). To be sure, our knowledge of Quintana Roo, the Mexican state lying north of British Honduras, and south of Yucatan proper, is very slight. Standley says that "of the flora of Campeche our present knowledge probably could be recorded on a single page of not very small

print." For the Petén district of Guatemala, the heart of the Maya Old Empire, there are only a few records resulting from a trip of Cook and Martin of the U. S. Department of Agriculture.

The part of the Yucatan peninsula which has been most adequately studied is the driest and floristically presumably the poorest, so there can be no doubt of Standley's great conservatism in stating that the whole flora would contain double the number of species so far accounted for. Since he lists only 1068 species the known flora is a very small one, and, as he says, compares very unfavorably with very much smaller areas such as the tropical Panama Canal Zone or even the temperate District of Columbia.

If it is borne in mind that the highland flora of Guatemala is similar in composition to the exceedingly rich southern Mexican highland flora, and that the latter passes into a large area of tropical lowland rain forest which in turn grades into the dry thorn-scrub of Yucatan, and that the Flora of Yucatan is based almost entirely upon the latter, we can readily see how much remains to be accomplished. Standley wrote in the preface to his Flora: "It is not probable that the botanical exploration of the region will be completed in the near future. Botanists, at least modern ones, like other naturalists, choose the pleasant and agreeable regions in which to work rather than those of prime botanic interest. It is an easy matter to indicate on a map the areas of tropical America in which the richest results could be obtained, but try to find a botanist who will explore them . . . Quintana Roo is still a sparsely inhabited territory because of the unfriendliness of its few primitive inhabitants towards strangers. Moreover it is reputed to be infested with malignant malaria. Campeche possesses large tracts difficult of access. It may be predicted with all confidence that for some time to come botanists who visit the Yucatan Peninsula will continue, as heretofore, to confine their travels to the usual tourist routes of the state of Yucatan, or to the more easily accessible portions of northern British Honduras."

Already Mr. C. L. Lundell, whose collections in the Orange Walk District of British Honduras have been mentioned, has gone to Campeche, where he is botanizing in the back country of a practically unknown district. Unusually valuable information is sure to result from his work, since a resident collector, watching the flora throughout the year, secures much that could not be obtained by an expedition.

The state of Tabasco is another botanically neglected part of the Maya area. The ferns are included in the "Pteridografia del Sur de Mexico" of the Mexican botanist Rovirosa. The same botanist made collections in other groups, but the flora as a whole is relatively unknown.

There have been recent collections in Chiapas by E. W. Nelson of the U. S. Biological Survey and by the archeologists E. and C. Seler. This last year Mr. Carl O. Erlanson made an important trip for the study and collection of economic plants, in behalf of the Office of Foreign Plant Introduction of the U. S. Department of Agriculture, but much of this important region remains botanically untouched.

We have now reviewed the status of botanical exploration in the area within which important ruins of old Maya civilization have been discovered. The Maya people and Maya influence extended farther northward, however; so it is desirable to include parts of the marginal states of Oaxaca and Vera Cruz in our survey. Oaxaca has been visited by some of the best recent collectors, notably by Pringle and E. W. Nelson, but it is especially fortunate in having a resident botanist of distinction who has devoted many years to the study of the flora—Professor C. Conzatti. His paper on the botanic geography of Oaxaca presents one of the first pieces of reasonably detailed vegetational mapping which we have for Mexico. Such a map, on a somewhat larger scale, is one of the objectives of the projected biological survey of the Maya area. Professor Conzatti's map of a state on the margin of the area is a substantial contribution.

In connection with vegetational mapping, it may be said that there will also be great need and opportunity for close ecological study of the successions which result in the reestablishment of typical forest on abandoned land. Formerly populous Maya sites are now covered with forest, which has all the characteristics that are commonly accepted as "primaeval." It even remains to be discovered whether at low altitudes in the Maya region there can be discovered any criterion for distinguishing primary from secondary forest. Since one of the chief results of a botanical survey, from the standpoint of the archeologist, will be to determine what land was formerly in cultivation, the importance of the ecological point of view is manifest.

An enormous amount of botanical work has been done in the state of Vera Cruz. Yet the discoveries that are being made still by Purpus have shown that the field is far from exhausted. Maxon indicated more than twenty years ago that from the standpoint of ferns the most valuable field work that could be done in tropical America would be a thorough combing of the middle altitudes in Oaxaca and Vera Cruz. What was true then is still in large measure true, not only for the ferns but for other groups as well, the reason being that the higher altitudes are more attractive to collectors.

At the north of the long coastal state of Vera Cruz, at the border of Tamaulipas, is the Huasteca region, an isolated island of the Maya area.

One of the first contributions to Mexican botany published in America, Asa Gray's paper on Ervendberg's plants from Tantoyuca, dealt with the flora of this region. Berlandier collected there also, and more recently Palmer, but from the ethnobotanical and linguistic point of view a thorough botanical going-over of the region ought to be most productive and should be one of the chief botanical objectives of the Maya project.

The whole of southern Mexico and Central America needs all the study that can be devoted to it on the economic side. As Blake has pointed out, the Mexican botanists have done nearly all that has been done in the way of recording the uses and names of plants. The botanists of Europe and America have done the purely taxonomic and descriptive work, but the two bodies of literature have remained largely uncorrelated.

The Maya area is presumed to be, and there is good evidence that it is, one of the two primary centers in which American agriculture developed. This is not to say that there were not other centers which enriched aboriginal argiculture with their share of cultivated plants. The Maya area, however, was preeminently the cradle of American civilization and one of the two regions (the other being Peru) whose native flora contributed the plants basic for agricultural and other utilization. This point has been brought out forcibly by Vavilov, whose recent expeditions in behalf of the Soviet Russian government have brought together an enormous wealth of economic plant material.

Vavilov has come to certain conclusions as a result of his explorations which are very significant indeed. These are: (1) that every primary center of indigenous culture developed not merely because of favorable living conditions in general, but in particular because of an especial wealth of wild economic plants whose products, at first merely gathered, were eventually secured more abundantly by taking them into cultivation; (2) that the modification of plants in cultivation consists primarily in the sorting out of recessive types which appear either as mutations or as segregates from hybrids; (3) that since man has disseminated most widely the most specialized cultivated types, the peripheral areas in the distribution of any economic species, or group of inter-related species, contain predominantly extracted recessive inbred types which, remaining isolated, have in large measure lost the possibility of giving rise to further useful variants; (4) that the original center, on the contrary, where the cultivated selected types remain in association with the wild progenitors, is the region where the greatest number of dominant characteristics will be preserved, where the number of varietal types will be the greatest, and to which modern agriculture may return for strains which will serve as new points of departure for plant breeding. In otherwise habitable regions which provided

the best sources of food, the civilizations of antiquity grew up, each at
first developing its own initial plant resources and eventually borrowing
from other centers.

Judged in accordance with these criteria it was in the southern part
of Mexico that the most basic plant of American agriculture, maize, origi-
nated. In this region the greatest diversity of varieties exists, and here
maize has been grown for ages under the most primitive agricultural con-
ditions—namely, in fresh forest clearings without irrigation. Since maize
obviously owes its persistance, in all of its known forms, to man's care,
and must therefore have originated from something that presumably still
exists, the most natural conclusion is that it has been derived from teosinte
(*Euchlaena mexicana*) the only plant with which it crosses freely and pro-
duces fertile hybrids. It must have originated in Mexico because *Euch-
laena* is not found farther south. Collins has shown that the Mexican
population of *Euchlaena mexicana* differs considerably from the one which
in Florida is considered the same species, and that the Mexican strains
can be duplicated among the hybrid combinations secured by crossing the
Florida *Euchlaena* with maize. It would therefore appear that much or
all of the population of *Euchlaena* in Mexico may represent the result of
interbreeding with maize, and, conversely, that whatever direct wild pro-
genitors maize may have had have been generally eliminated by hybridi-
zation with cultivated maize.

Collins has stated the objections that may be raised to the hypothesis
that maize arose as a mutation from *Euchlaena*. (1) Its characteristics do
not cohere as a unit in hybridization with *Euchlaena*. On the contrary,
the hybrid is resolved by segregation into a series of very different hy-
brid combinations. (2) Primitive man would not have observed and pre-
served an original mutation, since *Euchlaena* was of no use to him, and
would not have been cultivated. As Collins says, it is almost incon-
ceivable that the very small seed of *Euchlaena*, almost inextricably im-
bedded in a segment of woody rachis much larger than itself, could have
been used for food. We must agree with Weatherwax that there was once,
somewhere, a prototype of cultivated maize that had such characteristics
that it could have been directly of use as a food plant when man found it.

If we assume that such a primitive maize arose in the wild, very lo-
cally, as the result of interacting factors for which the necessary mutations
took place in different chromosomes and in different lines of descent in
Euchlaena (thus differing with Weatherwax), we arrive at a hypothesis
that seems to have much in its favor. Maize might then appear suddenly,
as though by immediate mutation, but really as a result of a rare fortui-
tous combination of factors. Having once appeared, even though it were

immediately submerged by crossing, maize would give rise to a heter-
ozygous germplasm from which the maize combination might repeatedly
and frequently appear by segregation. Some such phenomenon may have
come about as a population of wild maize existing only jointly with teo-
sinte, the maize individuals appearing presumably by segregation from
the hybrid combinations by iterative crossing in every generation, for the
maize plants, even though not contributing to the population by seed,
would contribute pollen for back-crossing of the hybrids. Since we know
from the vast number of Mendelian types in maize that the maize chromo-
somes are very mutable, there is no reason why the potential evolution
of maize varieties should not have been taking place while the maize
chromosomes were in teosinte combinations. If the association of charac-
teristics that distinguish *Zea* is due primarily to a certain fortuitous com-
bination of mutated factors of *Euchlaena* chromosomes and the *Euchlaena*
chromosomes are therefore not merely remotely homologous with *Zea*
chromosomes but actually interchangeable with them, there would seem
to be no reason why genetic analysis should not clear up the problem.
Investigators must simply devote themselves to the genetic study of teo-
sinte-maize hybrids with the same assiduity that they now devote them-
selves to the genetics of maize. The results have direct utility in neither
instance, and since the problem of the origin of maize is the most inter-
esting one presented by American agriculture and ethnobotany, it would
appear worth while for geneticists to shift their point of attack somewhat.
Perhaps Sereno Watson was not, after all, so far wrong when he de-
scribed a spontaneous maize-teosinte hybrid from Mexico under the name
Zea canina, considering it a wild maize.

Dr. Paul Weatherwax is about to leave for Mexico, where he will de-
vote himself for some months to assembling materials bearing on the prob-
lem of the origin of maize. His previous researches have given him un-
surpassed preparation for the undertaking and we will all wish him the
greatest of success. The student of the Maya area, it must be reiterated,
cannot give disproportionate attention to maize. Other plants were of
course important and the early civilization doubtless took into cultivation
or utilized in the wild scores of plants. Nevertheless maize was basic. Next
in importance came beans and squashes, and other crops were distinctly
subsidiary. This is not said to minimize in any way the value of finding
out all that can be found out about every useful plant, for facts regarding
any one of them may throw light upon early culture. Every botanist
should make a point of making such observations as those which Wilson
Popenoe published in his short paper on "the Useful Plants of Copan." It
is the sort of a critically annotated list which ought to be published for

as many localities as possible, since there is distinct danger in attempting
to draw conclusions regarding the economic botany of any large region
unless the geographic data are very precise. Vavilov has found fault with
O. F. Cook's list of the indigenous economic and domesticated plants and
animals of Peru on the ground that about half of them are introduced. His
own list for Central America and southern Mexico includes guayule, *Parthenium argentatum* of northern Mexico, which has only become an economic plant very recently and had no significance in ancient culture, *Agave lechuguilla*, an important fiber plant of Texas and northern Mexico, sotol,
Dasylirion durangense, which is merely the most southern member of a
North-Mexican group and is not cultivated, etc. In making up any list of
plants which may have served primitive man as the foundation of an
agricultural civilization, it is quite obvious that one must not associate
species which do not grow in the same very limited region. The occurrence
of lechuguilla in North Mexico is surely no argument for the primacy of
South Mexico as a culture center. Nevertheless, if used cautiously, Vavilov's hypotheses and methods should be of the utmost value in connection with the biological survey of the Maya culture area.

Now a few words with regard to the first expedition undertaken by
the University of Michigan. The objective was Uaxactun, in the Petén
district of Guatemala, where for seven years the Carnegie Institution has
been engaged in excavating the oldest city of the Maya Old Empire. The
site is reached by a trip across British Honduras to El Cayo, the head of
navigation by small launches on the Belize River. During the brief dry
season the Carnegie Institution maintains communication from El Cayo
with Uaxactun by mule trains, making a round trip as regularly as possible every nine or ten days. On account of late rains in 1931 it was impracticable to traverse the logwood swamps with sufficient equipment to
work efficiently until several weeks later than had been planned, but the
time was utilized to the best possible advantage by collecting and study
in British Honduras, where the work accomplished on the great pine area
known as the Mountain Pine Ridge (the "Great Southern Pine Ridge" of
some maps) was especially valuable.

The Michigan party consisted of Dr. Josselyn Van Tyne, ornithologist,
Dr. Adolf Murie, mammalogist, and the speaker, botanist. There had previously been some bird collections made in the Mountain Pine Ridge, but
in other fields of natural history little if anything had previously been
done. So the delay in reaching Uaxactun was not too serious a matter,
since the time spent there was adequate for making representative even
if far from complete collections. In tropical rain forests it is very difficult

indeed to collect rapidly, since herbaceous and other easily accessible plants are soon exhausted, leaving trees and lianas to be sought out when in proper condition for collecting and more or less laboriously secured by climbing or felling.

The botanical studies were primarily floristic this first season, since there was no opportunity in the practically unpopulated region about Uaxactun for contact with Mayas. The botanist did, however, arrange to have as one of his helpers an elderly Maya of El Cayo, whose parents were natives of the Petén near Benque Viejo. This man, Mercedes Chanec, was especially chosen because of his knowledge of plants. With his aid, and that of other speakers of Maya, a considerable vocabulary of plant names was obtained.

Ethnobotanical work must be stressed in the future whenever the expeditions have good contacts with the Maya population. In spite of almost minimal contacts the first year, a good start has been made. Some of the economic plants which seldom or never flower have been sent alive to the Michigan Botanical Garden to be grown for identification. The maize varieties were collected with especial care and referred for study to Professor R. A. Brink, of the University of Wisconsin.

One matter of especial interest in connection with the archaeological work will be the search of the plant cover of the ruins for economic plants which may be interpreted as vestiges of ancient cultivation. Only long experience can show what plants really belong in this category, but one is tempted to suspect that among them are the fine shrubby *Physalis* of the ruins of Uaxactun and the *Agave* which grows on the great temples at Tikal. The *aguadas* (water holes) are likewise likely to shield plants that are not truly indigenous, but owe their present distribution to human agency. One must not overlook similar possibilities among the plants of the forest, but here the problem is so complex that only wide travel and long experience in the region will enable one to judge of what in the present distribution of plants is natural and what has followed upon human occupation of the land. Here ethnobotanical problems merge into those of phytogeography and ecology.

With the first season's collections in hand, a bulky and interesting mass of material which no one botanist could identify and report upon in any reasonable length of time, it has been arranged, in order to deal with it promptly and have results for publication as soon as possible, to distribute much of the material to specialists for study. As many groups as we can handle efficiently at the University of Michigan will be studied by our own staff. The task of this Biological Survey of the Maya area has not

been undertaken lightly and would be impossible of accomplishment except for the cordial cooperation which seems to be assured at every hand.

UNIVERSITY OF MICHIGAN
  ANN ARBOR, MICH.

The progress of botanical exploration in tropical South America[1]

H. A. GLEASON

(WITH A TEXT FIGURE)

It was a prodigious task which faced the pioneer botanical explorers of South America. It is unnecessary to do more than remind you that tropical South America is of greater extent than the whole of the United States, contains the greatest expanse of rain-forest to be found in the world and the highest mountains of the western hemisphere. All of these have made the process of exploration exceedingly difficult in the past and even today travel away from the customary roads, the few railroads, or the navigable rivers is still slow, expensive, and often difficult. The diplomat and the salesman can now reach with ease any part of the continent which interests them; the engineer and the oil geologist can make their own roads as they go; but the poor botanist has still the same trouble in reaching the country which he wants to see as did his predecessors of a century ago. As a result, tropical South America, considered as a whole, is still very inadequately known botanically, notwithstanding more than a century of effort by some scores of collectors who have brought back many thousands of specimens to the herbaria of the world.

What do we mean by the expression adequately known? Let me illustrate by comparison. If one should collect flowering plants energetically for a full year in Ohio or Massachusetts, it is almost certain that he would find not one undescribed species. He might find a few, a very few, species which had not been previously known from that state. A similar year in Florida or Louisiana might result in a very few species unknown to science, but the number would certainly be less than 1 per cent of the total. The flora of these states is adequately, if not yet completely known. There are a few bright spots on the otherwise dark continent of South America where one might have the same experience, but in general the booty of an extended botanical trip still contains in round figures ten per cent of species unknown to science, and this rises to higher figures if the collector gets at all away from the usual routes of travel. Possibly a South American maximum was reached in 1928, when Tate climbed Mount Duida for the first time and brought back a collection in which nearly 70 per cent were new species.

A remarkable feature of tropical South America is the fact that collectors may travel repeatedly over the same route and still find different species, even of the larger and more conspicuous groups. Thus Poeppig, Martius, Spruce, Ule, and Tessmann collected at different periods along the Amazon in eastern Peru and all of them found numerous species unseen by the others, even though they must have often visited precisely the same localities. Nor did they exhaust the field, for the recent visits of Williams, Killip, and Smith to the same ground has resulted in the detection of scores of unknown species, and after them Klug, working over the same general localities, sends in still other species completely new to science. Schomburgk traveled back and forth over the savannas of northern Brazil and discovered numerous new species. Ule covered essentially the same ground and added many new ones. Tate followed Ule's trail almost exactly and discovered still others which none of his predecessors had found. This has been the continuous experience of botanists in most parts of South America for a century, so that we feel morally certain that we have by no means reached the end of botanical discovery, although we now approach it in a few limited districts. There are several reasons for this remarkable condition. One is the great luxuriance of the flora and the near impossibility of collecting all the plants which one sees. A second is the seasonal behavior of the flora, by which collectors visiting the same spot at different seasons have their attention directed to a different set of species. A third is the prevalence of trees, from which collecting is normally difficult and often impossible, and only a lucky chance gives some one man an opportunity to secure flowering specimens of some of the forest giants. A fourth is the difficulty of detecting the smaller species among the welter of larger plants. Thus Spruce collected several new species of the tiny Burmanniaceae, not one of which, to my knowledge, has ever been seen again. Still another cause is the sporadic distribution of the species. Two towns along the lower Mississippi, let us say a hundred miles apart, will have almost precisely the same flora, but two ports along the upper Amazon, no farther apart, will have a surprising difference in flora, even though the soil and climate are indistinguishable. And if a collector uses a small boat and stops off at the smaller Indian villages between the ports, as Klug and Williams have done, he finds still other kinds of plants.

Time does not permit even an enumeration of the numerous botanists who have risked their lives and prejudiced their health in these South American jungles and mountains for the cause of science, but a few have carried on exploration of such difficulty or such magnitude that they must be mentioned. Let me name first Joseph Jussieu. Attached to the French expedition to determine the length of a degree of latitude at the equator,

he left the party in 1747 and disappeared over the mountains to the un-known lands east of Quito. Three years later he reappeared in Bolivia, 1500 miles to the south, and lived there twenty-one years. What hardships he must have endured during three years in the hot lowlands I leave to your imagination; unfortunately he brought back few specimens. Bon-pland, always fragile in health and often an invalid, accompanied Hum-boldt on his long and strenuous exploration in tropical America 130 years ago, climbing to high altitudes in the Andes, braving the fevers of the Amazonian forests, and bringing back a rich collection which was the foundation of our knowledge of the Andean flora of Colombia and Ecuador. Others who deserve mention are Aublet, collecting (1762–1764) and los-ing his health in fever-ridden French Guiana and publishing his flora in 1775; Martius, exploring eastern Brazil, ascending the Amazon in 1819 and 1820 and later founding that monumental work, the Flora Brasiliensis; Schomburgk (1837–1841), crossing British Guiana in every direction and traveling on foot the whole length of the Pacaraima mountains; Spruce, living for fifteen years (1849–1864) among the Indians of the upper Ama-zon and in the mountains of Peru and Ecuador; Poeppig, exploring the tributaries of the Amazon in eastern Peru (1829–1832); Gardner, traveling far and wide (1836–1841) over inland Brazil; Mathews, living isolated and dying among the mountains of northern Peru (1833–1841). Beside these exploits, the achievements of such hardy explorers of North America as Kalm, Michaux, Nuttall, and Charles Wright are colorless. In fact, we may safely say that no other continent can present such a picture of devotion to botanical science in the face of hardship and danger.

Followed these pioneers a series of professional collectors of living plants and seeds for the gardens of Europe, who also collected herbarium material of great value. Chief among them were Funck, Schlim, Linden, and Lobb, all working in the Andes from Venezuela to Bolivia.

Still later, we find important work being done by a group of men resi-dents of the country and occupying scientific positions in the universities and museums of the developing continent. Of the numerous men of this category who have added much to botanical knowledge, I can mention only a very few: Huber, Hoehne, Ducke, Ule, of Brazil; Jenman of British Guiana; Pittier of Venezuela; Sodiro of Ecuador; Brother Ariste-Joseph of Columbia; Raimondi, Weberbauer, and Herrera of Peru; Buchtien of Bolivia. We can not afford to neglect André, the landscape architect and artist, or Lehmann, the German consul, both of whom collected thousands of plants of the greatest scientific value.

North Americans have turned their attention to South America only in the last few years. In 1918 the Gray Herbarium of Harvard University, the

National Herbarium of Washington, and the New York Botanical Garden began their cooperative investigation of the northernmost countries, from French Guiana to Ecuador. A few years later the Field Museum began an extensive study of the flora of Peru. Sponsored by these powerful institutions, and perhaps better equipped than most of their predecessors, numerous botanists have explored parts of South America and it is due chiefly to their efforts that the leading herbaria of our own country now have a larger and often a more complete representation of the South American flora than can be found in Europe. Among the men who have aided in this work I mention merely the names of Archer, Dahlgren, Hazen, Hitchcock, Killip, Macbride, Pennell, Rose, Rusby, Smith, Williams. In the meantime European interest has not lagged and collecting has recently been done in this field by Sandwith, Tessmann, and Snethlage, while the work of the Swedish botanists under the Regnell Foundation still continues in Brazil and the Dutch are active in Surinam.

If we could plot on a single map the various routes across South America which have been followed by these and other botanical explorers, we should find a remarkable meshwork of criss-cross lines, running in all directions and covering, in a general way, all parts of the continent. It would at the same time be quite apparent that there was a general tendency for the lines to converge toward certain centers of population and to overlie each other along certain well known trade routes. This is only natural. An explorer landing from an ocean voyage in a new continent, surrounded by a new flora, gives way to his enthusiasm, and collects immediately at the seaport, forgetting that numerous other botanists have collected there before him. Rio, Pará, Cayenne, Paramaribo, Georgetown, Caracas, Maracaibo, Cartagena, Guayaquil, and Callao have all been botanized repeatedly. When this same botanist starts inland on his explorations, he again tends to follow established trade routes for as long a distance as possible on the way to his destination, and again his collecting tends to overlap with that of his predecessors. This is not said in criticism. Quite on the contrary, it is this repetition of work in the same territory that has been necessary to discover and collect the flora. Even yet that work is not absolutely complete, not even for small districts about the seaports, or for the frequented trade-routes. I venture to say that there is not in all tropical South America a tract of a hundred square miles with its flowering plants all known and listed. Finding the first half of a flora is easy. Finding the next forty per cent is interesting, having the excitement of discovery without the necessity of too great exertion. Finding the last ten per cent means long continued work, and an effort probably quite out of proportion to the interest or value of the results.

Reverting to our imaginary map, we would notice on it, outside these lines which botanists have followed, and spots where collecting has been rather intense, that the distance between lines, the width of the meshes in our network of routes, varies greatly, and these meshes represent unexplored areas. Any one of these meshes may of course contain hidden in it some unknown species, or some plant not yet collected in the general region, but the proportion of such unknown or undiscovered species is naturally greatest in the larger ones, and will be particularly high in those large ones which also contain a type of environment not represented elsewhere. Any good herbarium will show, and personal experience will verify, that two stations in the tropical rain forest fifty miles apart will show a considerable variation in their flora, even though the climate is the same in both, while a change in climate or soil, due to altitude or geology, is associated with much greater changes in the flora than we are accustomed to in the temperate zone.

An immense amount of biographical research would be necessary to construct such a map as I have described, showing all the collecting routes in South America, but a different sort of map may be more easily prepared and will probably be more useful to us. Let us divide South America according to our present knowledge of its flora. Four grades of knowledge may be arbitrarily distinguished, which I shall describe briefly, beginning with the highest. In this the flora has been repeatedly collected until by far the greater part of it is known. New species are still discovered occasionally, to be sure, and additions are often made to the known flora, but still the flora may be called adequately known. In such regions the plants are known probably as well as they were in the southern states when Chapman wrote his flora, or possibly even better, say as completely as in Alabama when Mohr wrote his Plant Life of that state. Repeated collecting has made these areas well represented in herbaria so that most species are illustrated by ample material. There is opportunity for further work, of course, but it will result in the completion of our knowledge of existing species rather than in additions to the flora.

In the second group I place those areas which have been repeatedly botanized but from which a considerably smaller part of the probable total flora is known. Many additional species will be added to herbaria from such regions, numerous new species may still be expected. Representation of these areas in American herbaria is not always good and further exploration would be greatly to their profit. That is especially the case in some particular spots from which numerous types have been collected. Re-collecting in the same locality would add many extremely valuable topotypes to our collections.

In the third class we may place the greatest part of tropical South America. Here we know comparatively little of the ranges of species, either in altitude or latitude. Every botanical expedition across such areas brings back a quantity of undescribed species as well as numerous others not previously known from the region.
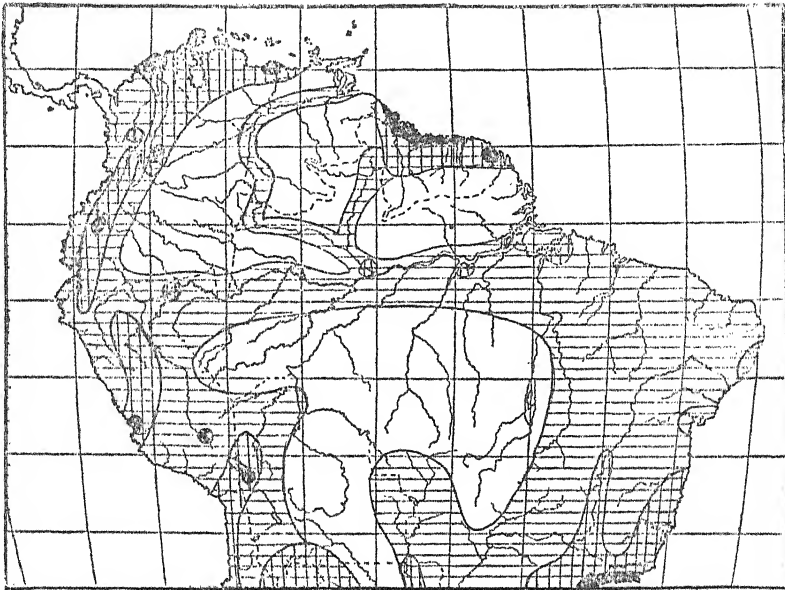
Fig. 1. Progress of botanical exploration. Black—adequately known. Cross-hatched — fairly well known. Lined—poorly known. Blank—virtually unknown.

Lastly, the fourth and lowest class includes those regions which have never been explored at all or which have been traversed but once or twice. Here almost every collection represents an extension of a known range or a species unknown to science. These are the places which will yield the richest results to botanical explorers, the areas to which every collector wishes to lead his next expedition.

None of these four can be defined quantitatively and my division of tropical South America among them is naturally open to criticism, yet I believe that the map will serve to show in a fairly accurate way how they lie.

In the first category I place a fair-sized area in southern Brazil, about the cities of Rio and Sao Paulo, the island of Trinidad, the coastal lands of British and Dutch Guiana and near the mouth of the Magdalena River in Columbia; also much restricted areas surrounding the cities of Cayenne, Caracas, Bogota, Quito, Lima, Cuzco and La Paz. Here and here only, do we have, in my opinion, an adequate knowledge of the phanerogamic flora.

The second class in naturally larger in size. I place in it part of the state of Minas Geraes, north of Rio, a fair-sized area around the city of Pará, smaller areas around Santarem, Manáos, and Iquitos, the coast of French Guiana, a fairly wide strip just back of the coast in Surinam and British Guiana, the coastal Andes of Venezuela from somewhat east of Caracas to south of Maracaibo, connecting with a region in Columbia north and northeast of Bogota, a smaller region in the south end of the Cauca Valley in Colombia, extending through Ecuador to Guayaquil; a good share of the mountain mass of central Peru, the Yungas region of northern Bolivia, the coast of northern Chile, and a few other isolated areas elsewhere. If I were in charge of one of the smaller American herbaria and desired to build up a representative collection of South American plants, I should send my first expedition into some of these places.

The third class covers the largest part of the area. Here I place the rest of eastern and southern Brazil south of the Amazon, most of the wooded area of the Guianas, the savannas of southern British Guiana and Mount Roraima, the immediate valleys of the Amazon, Branco, Negro, and Orinoco, and all of the Andean region not included in the two preceding groups. Of this whole area, the part most needing exploration is the arid inland region of northeastern Brazil.

Then we have left the unknown fourth. In Brazil this includes a strip of country north of the Amazon and the lowlands of the Acre territory, in the Guianas the unknown mountains between them and Brazil; in Venezuela the whole southern half; in Colombia the savannas and forests of the eastern lowlands; in Ecuador the eastern triangle; in Peru a bit of country bounding the Acre territory of Brazil; in Bolivia the eastern lowlands, off to the Gran Chaco country at the southeast.

And now a word about the future. If the botanical institutions of the United States wish to assume a leading part in the study of South American botany, a position toward which they have been striving for several years, two campaigns are necessary. Most of the known species of South America are based on type specimens deposited in European herbaria, seldom with duplicates in any herbarium on this side of the Atlantic. We must know accurately what these species are, so that more recent collections of the same species can be properly labeled in our own herbaria and other but somewhat similar species can be properly differentiated. To do this at present, we must usually depend on printed descriptions, which are often fragmentary, neglecting various structural features which the earlier botanists considered of no significance. We must take steps to get into our collections authentic material of these older species, and the best way to accomplish it is to send expeditions into the field to collect intensively at the

very places where these species were originally discovered. We should re-
trace the route of Humboldt, collect again extensively at Tarapoto, at
Chachapoyas, at Quito, on the upper Rio Negro, and in many other places
where botanical history has already been made. Our specimens should
then be compared with the greatest care with the types in European her-
baria, and a series of substitute types, or topotypes, prepared to illustrate
these old species in America. In this connection I may mention that the
great series of photographs of types prepared by Dr. Macbride and dis-
tributed by the Field Museum will be of great value, while the collection of
Spruce's plants recently received by the New York Botanical Garden
brings to this country a great number of duplicate types.

The second campaign is one of further exploration. While the great
collections from Colombia at the National Herbarium, from Peru at the
Field Museum, from Bolivia at the New York Botanical Garden, are all
noteworthy, not a single country in South America is as yet really well
represented in any American herbarium. Except in those few and small
areas to which I assigned the grade of one in my discussion a few minutes
ago, exploration in any part of tropical South America is desirable and
profitable.

In looking forward to future fields for exploration, our thoughts natu-
rally turn to the regions which are as yet unknown botanically. They have
remained unknown so long chiefly because of the difficulty in reaching
them. Physical difficulties can be surmounted and we have plenty of
young men anxious to show what they can do. Financial difficulties are
more serious and, in my opinion, can best be met by cooperation among
interested institutions. What one institution can not do alone, several can
do by working together. South American collectors must be trained and
encouraged, and a market assured for their collections. It is only by work-
ing shoulder to shoulder that the unknown areas on our map can be ap-
preciably reduced.

THE NEW YORK BOTANICAL GARDEN
   NEW YORK, N. Y.

An international program for a world-wide study of woods[1]

Samuel J. Record

It is a matter of common knowledge that woods are not all alike. Their differences in composition, color, odor, grain, texture, weight, strength, and durability are of much economic importance in the timber industry. What is not so generally appreciated is that there are no two woods exactly alike. In a great many cases it is now possible to identify a wood with certainty as to its genus, frequently as to its section of a genus, and sometimes as to its species or even variety. The number of such cases is increasing so rapidly that it is only a question of time until no exceptions remain.

Delay in approximating this goal may be ascribed mostly to the lack of suitable material for study. Some of the earlier German and French anatomists made the most of the specimens at their disposal, but for nearly all except the commonest trees they had to work with twigs taken from herbarium sheets. It is only in recent years that serious effort has been made to get wood samples from the main stem of trees from which herbarium material is taken. This calls for a new type of collector who realizes that the trunk of a forest tree equals the leaves and flowers in scientific interest and surpasses them a thousand times in economic value.

The student of wood looks to the systematic botanists to classify and name his plants, and he has no intention of setting up a separate classification. He is therefore keenly interested in what systematic botanists do and would appreciate a reciprocal interest on their part. He deplores the loss of time and effort necessary to bridge the gaps the ordinary collector leaves in our knowledge of tree and forest. Think what it would mean to science and industry if every herbarium specimen of a tree were accompanied by a sample of the wood! Is it too much to ask the present generation of botanists to attempt some atonement for the shortcomings of their predecessors? Why not widen the field of systematic botany and increase its usefulness? Why shouldn't botanists seek to name the whole tree and not just a few fragments of foliage and flowers? The work will be harder for the original collector, but it will not need to be done all over again. And if the wood of a type tree is missed, no amount of subsequent collections can ever quite make good the loss.

The task of getting a comprehensive general collection of woods for systematic study is made especially difficult by the fact that most arbores-

cent species occur in the poorly accessible forests of the tropics. Scientific interest alone is scarcely incentive enough for sending costly expeditions after wood samples. But with reduction in the timber supply of the North Temperate Zone has come opportunity for the profitable exploitation of the vast tropical forests. The woods of the tropics are different in kind and technical properties from those with which civilized man has been so long familiar, and their introduction into the trade is usually a slow and difficult process. European countries with colonial possessions, as well as some of the tropical countries themselves, are attempting to hasten this process and to stimulate their export trade. To this end they have built research laboratories for the thorough investigation of their timbers so that the manufacturer can employ them to the best advantage. Such work is of doubtful value unless the identity of every test specimen is known, hence each laboratory and research institution becomes a center for the building up of study collections of authentic samples. Fortunately such collections are not limited to the few species known to have commercial value, but often include all the different kinds of woods possible to obtain. For instance, at the Forest Research Institute at Buitenzorg, Java, are more than 15,000 wood samples from all parts of the Dutch East Indian Archipelago, each specimen authenticated by herbarium material from the same tree. In that collection are representatives of more than 500 genera of about 100 families.

Most of the best wood collections are regional, and much of the research work is with geographical groups rather than by families. I believe the time is at hand to begin the preparation of a comprehensive work on the woods of the world, dealing with them systematically by families and genera. The easiest way to accomplish this is to get a number of scientists to work on monographs of related groups or families. The principal incentive needed is the material. It is hopelessly impossible to supply samples of all the species of any but the smallest families, but enough of the genera are represented in the different collections of the world to justify preliminary studies, and several of these are now well under way.

With this general object in view we are trying to make the Yale collection of woods as rich in genera as possible and are offering classified groups of specimens to competent research students anywhere. We now have over 20,000 fully catalogued samples representing about 6300 named species of trees of nearly 2000 genera of almost 200 families. They have been obtained in the following manner: (1) By members of the School staff, sometimes in cooperation with concerns, such as the United Fruit Company and the Firestone Plantations Company, which are interested in tropical development; (2) by resident botanists to whom subventions have been

granted for collecting excursions in their own countries, for example in the Brazilian Amazon region, in the mountain range near Santa Marta, Colombia, and in the Western Cordillera of Ecuador; (3) by company employees, school teachers, missionaries, prospectors, and others in out-of-the-way places who find collecting a pleasant hobby; (4) through purchase and exchange and through gifts from innumerable sources. Other institutions have been very generous in contributing duplicates from their collections, and in this way they have the assurance that their woods will be included in any extensive systematic work without interference with their own intensive or regional investigations.

Our procedure for making specimens available for study is very simple. From a family-and-genus catalogue of material on hand, the investigator makes his selection, and cuttings large enough for sectioning are sent to him, along with copies of the catalogue cards. In order to encourage further cooperation and also to avoid unintentional duplication, notice of each project undertaken, together with the name and address of the investigator, is published in our quarterly magazine, *Tropical Woods*, which has a circulation of about a thousand copies and reaches nearly all those interested in its field. This publication also contains original articles and notes, descriptions of new species discovered by Yale collectors, and a digest of the current literature. It aims to encourage collectors, to promote research, and to provide a readily accessible file of useful information and references which otherwise might escape notice or not reach students who lack adequate library facilities.

This is all very well so far as it goes, but it falls far short of meeting the real demand of the situation. There is need for a more general pooling of materials, for freer interchange of ideas, and for standardizing terminology and descriptions. There is need for better textbooks and manuals and for better training in the schools. There is need for closer cooperation with systematic botanists, paleobotanists, organic chemists, and others concerned directly or indirectly with woods. In short, there is need for some sort of international organization which can deal with the study of wood in all its ramifications.

With this in mind, two British scientists and myself proposed that a conference of wood anatomists be held on the occasion of the Fifth International Botanical Congress in August, 1930. My colleagues were Dr. L. Chalk, of the Imperial Forestry Institute at Oxford, and Mr. B. J. Rendle, of the Forest Products Research Laboratory, Princes Risborough. There were three public sessions at Cambridge and it was decided to form an International Association of Wood Anatomists. Owing largely to our inexperience in such matters, the association was not perfected, but the basis

for it was established and an organizing committee of nine appointed, consisting of representatives of Australia, Belgium, France, Germany, Great Britain, Netherlands, and the United States.

A second conference was held at Paris on July 4, 1931, in connection with the Congrès International du Bois et de la Sylviculture. The constitution recommended by the Organizing Committee was adopted. The first three articles are as follows:

1. The Association shall be called the International Association of Wood Anatomists.
2. The object of the Association shall be to advance the knowledge of wood anatomy in all its aspects.
3. The activities of the Association shall be:
    (a) To interchange ideas and information through correspondence and meetings.
    (b) To facilitate the collection and exchange of material.
    (c) To work toward standard terminology and descriptions.
    (d) To stimulate the publication of scientific articles and abstracts.
    (e) To encourage and assist the study and teaching of wood anatomy.
    (f) To engage in any other activity consistent with the object of the Association.

Three classes of members are provided for—namely, ordinary (or voting), corporate, and honorary. The affairs of the Association, including election of members, are administered by the council of not more than twelve ordinary members elected every three years. The council appoints a secretary-treasurer who is directly responsible to it. There are no other officers, as it was considered desirable to make the organization as simple as possible. The scope of the Association was purposely limited to the field of wood anatomy, as the sponsors did not care to assume responsibility for the larger and more elaborate organization necessary to include the several branches of wood technology.

No members were elected at the Paris meeting, but power to select the initial group was delegated to the Organizing Committee. This committee subsequently invited 27 members to join with it in founding the Association in accordance with the constitution. These charter members, 36 in all and representing 15 different countries, are at the moment balloting for the councilors who will direct the affairs of the Association for the first three years. By the end of that time there should be a membership of at least one hundred.

In the meantime the Organizing Committee has not confined its attention to devising a machine. On the contrary, it has anticipated some of the problems with which the Association will be concerned and has started cooperative work upon them. One of these is the preparation of a Manual

of Wood Anatomy. As a first step a glossary of terms used in describing woods was compiled in six languages and forwarded to experts in different countries for corrections and suggestions. Upon the basis of the returns, a revision was made and given a wider circulation, and a second revision will soon be issued for still further consideration and for translation into several more languages. At the same time certain details of wood structure, proposed standards for measurements, etc., have been assigned to individuals for special study. Good photomicrographs and drawings are being assembled for possible use in the manual, as it is intended to have every feature so fully illustrated and labeled that the meaning of every technical term will be clear. All terms in common usage will be defined and their equivalents in different languages will be given in the polyglot glossary. Other sections of the manual will deal with microtechnique, bibliography, and subjects to be determined, each part to be prepared under the direction of a specialist in that field.

Another undertaking, to be started immediately, is the compilation of lists of wood specimens which various institutions are willing to make available to members of the Association engaged on definite research problems. Organized effort will be made to increase the amount of authentic material. In this connection it is hoped that more systematic botanists will come to realize that within the trunk of a tree may be concealed the keys to some of their own taxonomic problems, and will modify their field collections accordingly. The Association needs all the good material it can possibly get, especially of the less common trees and the larger shrubs and woody vines. The results of the study of these materials will contribute to a general fund of knowledge which can be drawn upon to advantage by systematists, paleobotanists, foresters, timber dealers, wood users, and all who are concerned with forests and forest products.

It is with these ideas in mind that several of us in different parts of the world have decided to pool our resources and activities for the advancement of the knowledge of woods. Both personally and in my official capacity as secretary of its Organizing Committee, I wish to thank you for this opportunity to introduce to the scientific world the International Association of Wood Anatomists and to solicit for it your sympathetic interest and good will.

YALE UNIVERSITY SCHOOL OF FORESTRY
NEW HAVEN, CONN.

INDEX TO AMERICAN BOTANICAL LITERATURE
1920–1931

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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Organization and light relations in Polysphondylium

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In my account of the processes by which the integration of the uni-
cellular myxamoebae into pseudoplasmodia and sorocarps is brought
about, I have given data as to the general range of their variation in form
and size (Harper, 1929). In these studies considerable evidence was ac-
cumulated that *Polysphondylium* can develop and mature its sorocarps in
either the ordinary alternation of daylight and darkness or in continuous
darkness. Other students have noted this fact and it is also generally re-
ported—Van Tieghem (1880), Brefeld (1869, 1884), Olive (1902), Potts
(1902)—that both *Dictyostelium* and *Polysphondylium* are positively pho-
totropic under ordinary conditions of one-sided illumination. I have con-
firmed this fact by repeated observations, though I have not so far under-
taken quantitative studies of the effect of varying intensities or wave
lengths of light on the degree and nature of the phototropic response.
Plants like *Polysphondylium* in which the processes of growth and cell
multiplication are separated from those of morphogenesis and differenti-
ation are favorable for the further analysis of the specific effects of environ-
mental stimulation on the various phases and stages of growth, integra-
tion, organogenesis and histogenesis and the development of the plant as
a whole. The experiments which I shall here describe deal with the mor-
photic relations of light as shown in the size and form of plants grown in
relatively continuous darkness as compared with the size and form of
plants grown under ordinary conditions of the alternation of day and night
in the laboratory. Potts (1902) has reported that plants of *Polysphondylium*
grown in darkness are larger than those grown in light, and Stameroff
(1897) finds that light has a differential effect on the vegetative and
fertile hyphae of *Mucor*.

My intention in not at once comparing plants grown in continuous
darkness with others grown in continuous light was to determine, as far
as possible, the effects on growth and morphogenesis of relatively contin-
uous darkness as compared with those obtained under the ordinary condi-
tions of development of the plants in nature. The cultures were grown in
ordinary dung decoction with 2 per cent agar in Petri dishes. The Petri
dishes were inverted and stacked under two bell jars. In all but one of the
experiments (no. II) the two bell jars were placed on a shelf about five feet
from a south window. In experiment II the cultures grown in light were
placed on a shelf much nearer the window. One of each pair of bell jars was
covered with a black cloth and the other was left exposed to the alternating

diffuse daylight and darkness of the laboratory. The room temperatures ranged from approximately 22° to 26° C. The cultures under the covered bell jar were exposed to daylight for a few minutes while being examined each day for general rate of development. The black cloth covering did not exclude all light. The object of the experiment was, as noted, to test the behavior of the plants under somewhat accentuated but similar conditions to those which might occur in nature as a result of chance in the distribution of the spores and their development in more or less shaded locations. No attempt was made to achieve an absolutely equivalent inoculation of each Petri dish. The spores for a given experiment were sown by picking up entire sorocarps from a single culture and dragging them across the agar, the point of the needle or forceps dipping deep enough to form a roughened streak in the agar surface. The first crop of sorocarps in such cultures is quite regularly formed along these streaks. This facilitates the counting of the plants, whorls per plant, branches per whorl, etc.

The first series was started April 14, 1929. It consisted of sixteen cultures, eight in alternating day and night, and eight in relatively continuous darkness. The Petri dishes were stacked, as noted above, under two bell jars which, with one exception, were placed side by side on a shelf about five feet from a south window. As further noted, one of the bell jars was covered with black cloth and the other left exposed to the diffuse light of the laboratory. One culture of the first series grown in the dark was accidentally broken on April 17, so that the final records for this series were taken from seven cultures. One culture in the corresponding series grown in alternating light and darkness failed to develop any plants, so that the final records for this lot also were taken from seven cultures. For brevity I shall speak of the two series as those in light and those in darkness respectively, and they are also indicated in the tables by the letters L and D. The number of cultures ranged from four to ten in each experiment, and the observations were continued from April 1929 to January 1930. The rate of development of the plants in all six of the experiments involving a total of 99 cultures was about the same.

The spores germinated, multiplied by division, and passed into an encapsuled and clumped stage within about twenty-four hours from the time they were sown. So far as I can find this encapsuled and clumped stage has not been hitherto described. I shall give figures and descriptions of it in a further paper. On the second day as a rule the creeping together (synallaxis) and the building of sorocarps (anallaxis) began. On the third day sorocarps were generally present in most of the cultures, and records for number of plants, number and order of whorls, and number of branches per whorl were generally taken from the fourth to the sixth day.

The number of sorocarps continues to increase for several days but the difficulty of getting accurate records also increases as the plants fall over and become tangled together. The sorocarps do not of course increase in size after they are once formed, so that a record of completed sorocarps taken within a few days of the time when they begin to form may be regarded as a fair average for the crop. It will be noted that the total number of plants recorded as having relatively large numbers of whorls (from 12 to 21) are from the later experiments. This is due in part at least to increasing skill in manipulation, whereby cultures with larger numbers of well distributed plants were produced, and to the resulting greater facility in making the counts of plants, whorls, and branches. The difficulty of following out the individual plants when they come to fall over and lie criss cross is considerable, and fewer of these larger plants were recorded from the earlier cultures. However the relative number of plants, whorls, and branches in the light and dark cultures respectively are fairly consistent. As shown in table.1 in each of the six series there is a smaller total number of plants and a smaller average number of plants per culture in the cultures grown in relative darkness than in the corresponding cultures grown in alternating day and night, and for the whorls and branches per plant a reverse tendency is shown. In each of the six series the higher average numbers of whorls per branched plant, the larger numbers of branches and the higher average numbers of branches per branched plant are found in the cultures grown in relative darkness. This holds true also whether, as in experiments II, III, IV, and VI (table 1), correction is made for the discrepancy of one in the number of cultures in light and darkness respectively. There is also a consistent excess in the number of unbranched plants in the light cultures as compared with those in darkness, with the single exception of experiment III.

As noted, the general type of erect radially and metamerically symmetrical organization and the method by which the integration and differentiation of the myxamoebae is brought about are described in a former paper (1929). The general plan of organization duplicates that of one of the higher cormophytes, except that there is no root system in *Polysphondylium*. Such plants grown in abundance in Petri dish cultures are favorable material for the quantitative study of the number and dimensions of the stipes, nodes and internodes, whorls of branches, terminal segments and sori, and the problems of symmetry of the plant as a whole. In the present paper I am presenting data as to the range in number of the whorls and branches of the sorocarp and the effect of light on the development of such structural elements.

TABLE 1

Summary of total cultures, plants, whorls, and branches

EXP.	CULT.		TOTAL PLANTS				RANGE				UNBRANCHED PLANTS				BRANCHED PLANTS	
			NUMBER		AV. PER CULT.		L		D		NUMBER		AV. PER CULT.		NUMBER	
	L	D	L	D	L	D	MIN.	MAX.	MIN.	MAX.	L	D	L	D	L	D
I	7	7	508	346	72.57	49.42	31	92	39	61	328	130	46.85	18.55	180	216
II	5	4	221	131	44.3	32.7	19	70	18	55	158	51	31.6	12.75	63	80
III	9	10	274	267	30.44	26.7	21	38	9	50	65	75	7.22	7.50	209	192
IV	9	9	354	204	39.33	22.66	17	76	4	39	80	31	8.88	3.44	274	173
V	10	10	887	317	88.7	31.7	13	190	12	67	260	45	26.00	4.5	627	272
VI	10	9	696	304	69.6	33.7	31	126	13	66	134	22	13.4	2.49	562	282
Totals	50	49	2940	1569	58.8	32.02					1025	354	20.5	7.22	1915	1215
Grand Totals			4509								1379				3130	

(*Continuation*)

EXP.	BRANCHED PLANTS		WHORLS				BRANCHES						AV. BR. PER PL. FOR ALL PLANTS	
	AV. PER CULT.		NUMBER		AV. PER BR. PLANT		NUMBER		AV. PER BR. PL.		AV. BR. PER WHORL			
	L	D	L	D	L	D	L	D	L	D	L	D	L	D
I	25.71	30.85	363	863	2.01	3.99	864	2097	4.8	9.7	2.38	2.42	1.70	6.06
II	12.64	20.00	120	317	1.90	3.96	237	828	3.76	10.35	1.97	2.56	1.07	6.32
III	23.22	19.2	793	1028	3.79	5.35	2091	2595	10.00	13.51	2.62	2.52	7.63	9.71
IV	30.4	19.22	1183	1071	4.31	6.19	2391	2385	8.72	13.78	2.02	2.22	6.75	11.69
V	62.7	27.2	2372	1752	3.78	6.44	4916	3533	7.84	12.98	2.07	2.01	5.54	11.14
VI	56.2	31.3	2301	1935	4.09	6.86	4560	4126	8.11	14.63	1.98	2.13	6.55	13.57
Totals	38.3	24.79	7132	6966	3.72	5.73	15059	15564	7.86	12.80	2.11	2.23	5.12	9.91
Grand Totals			14098				30623							

The metameric segments of *Polysphondylium* may be compared structurally with such elements as the phytons (Gaudichaud, 1843; Velenovský, 1905) each consisting of a node, whorl of branches, and an internode of the stipe as in the organization of the higher plants. The range in number of such units which can be combined in a single plant and the relative numbers of plants with each possible number of phytons which will be found in a mixed population such as is produced in Petri dish cultures are shown in tables 1–4.

MORPHOGENESIS AND PHOTOMORPHOSIS

The total number of plants whose structural organization was recorded in the six experiments was 2940 in the light cultures, and 1569 grown in relative darkness, as shown from the summary in table 1. The range in total plants in the six experiments is from 221 plants (exp. II) to 887 plants (exp. V) in light, and from 131 plants (exp. II) to 317 plants (exp. V) in darkness. The average number of plants per culture for the six experiments is 58.8 in light to 32.0 in darkness. The range in the average number of plants per culture (table 1) for the plants in the cultures in alternating day and night was from 30.4 (exp. III) to 88.7 (exp. V). In darkness the range was from 22.6 (exp. IV) to 49.4 (exp. I). The range in total number of plants recorded per culture for the whole series in the light was from thirteen in culture 605 (exp. V) to 190 in culture 598 (exp. V). The range for the whole series of cultures in darkness was from four in culture 505 (exp. VI) to 67 in culture 612 (exp. V).

In my cultures of *Polysphondylium*, as noted in my former paper (1929) there was always a considerable number of unbranched plants (*Dictyostelium* type). So far as tested, cultures from these gave no different results than those from branched plants. The total number of unbranched plants in the six experiments was 1379. The total number of branched plants was 3130. Of the unbranched plants 1025 were produced in the light cultures to 354 in the dark cultures, an average per culture respectively of about twenty to seven. Of the branched plants 1915 were produced in the light cultures to 1215 in the dark cultures. The averages per culture were respectively about thirty-eight for the light and twenty-four for darkness.

In table 2 the plants are grouped according to the number of whorls of branches per plant, and the extreme range is from plants with a single whorl of branches, of which there are 521, 377 in the light cultures to 144 in the dark cultures, to plants with twenty-one whorls of branches, of which there are but two, one in a light culture and one in a dark culture. The numbers of plants in the groups between these extremes form a series with its high point (585) in the group with two whorls of branches, 419 in

TABLE 2

Plants grouped according to number of whorls per plant

NUMBER OF PLANTS PER GROUP

EXP.	CULTURES		TOTAL PL.		1		2		3		4		5		6		7		8		9	
	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D
I	7	7	508	346	71	25	62	34	32	40	7	38	5	21	2	33	1	15	—	4	—	4
II	5	4	221	131	28	9	21	21	10	14	1	11	2	5	1	4	—	7	—	4	—	2
III	9	10	274	267	22	32	44	36	49	17	26	21	26	12	21	16	9	11	4	6	5	6
IV	9	9	354	204	40	21	51	21	48	17	39	11	28	20	17	7	14	15	5	11	8	11
V	10	10	887	317	127	30	128	24	114	21	77	30	53	32	40	18	26	13	10	19	14	21
VI	10	9	696	304	89	27	113	30	95	26	85	27	49	16	44	23	19	20	15	22	18	24
Totals	50	49	2940	1569	377	144	419	166	348	135	235	138	163	106	125	101	69	81	34	66	45	68
Grand Totals	99		4509		521		585		483		373		269		226		150		100		113	

(*Continuation*)

EXP.	10		11		12		13		14		15		16		17		18		19		20		21	
	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D
I	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
II	—	1	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
III	1	6	—	8	4	4	2	4	—	4	1	3	1	4	1	—	—	—	—	2	—	1	—	1
IV	6	8	6	14	3	2	3	6	2	3	1	3	—	2	1	4	1	1	1	—	—	—	—	—
V	16	23	11	7	4	11	3	7	—	3	—	3	—	—	—	—	1	3	—	2	—	1	1	—
VI	10	10	5	12	—	7	5	6	4	9	3	4	2	5	—	6	2	4	—	—	—	2	—	—
Totals	33	49	22	43	11	25	13	23	6	19	5	13	3	11	2	10	3	8	1	4	—	4	1	1
Grand Totals	82		65		36		36		25		18		14		12		11		5		4		2	

the light cultures and 166 in the dark cultures. Only ninety-one out of 4509 plants have fourteen or more whorls each. Over one-third (1106) of the total of 3130 branched plants are in the groups with one and two whorls of branches. One-half (1565) of the total number of branched plants would not include all of the groups with one, two, and three whorls, which total 1589 plants. The average branched plant in the light cultures has about 3.72 whorls against 5.73 whorls per plant in the cultures in darkness (table 1). The average number of branches per whorl in the light and dark cultures are respectively 2.11 and 2.23 (table 1). Whether the plants as grown in inverted dung agar Petri dish cultures are more or less luxuriant than those occurring in nature in the soil and on dung must be determined by culturing them further under controlled conditions as to substratum, moisture, etc. From the largest single group with two whorls of branches the number of plants per group diminishes continuously with the increasing number of whorls except that the group with nine whorls (113 plants) is larger than the group with eight whorls (100 plants) and the groups with twelve and thirteen whorls of branches show the same number of plants, (36). For the first six groups the number of plants in the light cultures is consistently larger, but from the seventh group to the twenty-first group the situation is reversed, and the numbers of plants in the dark cultures taken by groups are consistently larger, except that in the group with twenty-one whorls of branches there is one plant each in both the light and dark culture. The influence of light in increasing the number of plants and diminishing their size, as indicated by the number of whorls of branches which they bear, is thus shown quite consistently. If the series were plotted the graphs would cross each other at the seventh group.

The total number of whorls in each group for the light and dark cultures is given in table 3. The largest number of whorls for a single group (1492) is found in the group with four whorls per plant. In the cultures grown in light the largest number of whorls is in the group with three whorls per plant (1044), and in the case of cultures grown in darkness the largest number of whorls (612) is in the group with nine whorls per plant.

In the cultures grown under conditions of alternating day and night as in the case of the plant numbers, the number of whorls per group is consistently higher up to the sixth group, and from there on the relation is reversed and the number of whorls per group is consistently higher in the cultures grown in relatively continuous darkness, except in the single case of the two plants with twenty-one whorls. The total number of plants produced in the light is upward of twice that produced in the dark (2940 to 1569) (table 1). The total number of whorls is larger in the plants grown in the light by only 1+ per cent (7132 in light to 6966 in darkness).

Whorls grouped according to number of whorls per plant

EXP.	CULTURES		TOTAL WHORLS		NUMBER OF WHORLS PER GROUP																	
					1		2		3		4		5		6		7		8		9	
	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D
I	7	7	363	863	71	25	124	68	96	120	28	152	25	105	12	198	7	105	—	32	—	36
II	5	4	120	317	28	9	42	42	30	42	4	44	10	25	6	24	—	49	—	32	—	18
III	9	10	793	1028	22	32	88	72	147	51	104	84	130	60	126	96	63	77	32	48	45	54
IV	9	9	1183	1071	40	21	102	42	144	51	156	44	140	100	102	42	98	105	40	88	72	99
V	10	10	2372	1752	127	30	256	48	342	63	308	120	265	160	240	108	182	91	80	152	126	189
VI	10	9	2301	1935	89	27	226	60	285	78	340	108	245	80	264	138	133	140	120	176	162	216
Totals	50	49	7132	6966	377	144	838	332	1044	405	940	552	815	530	750	606	483	567	272	528	405	612
Grand Totals	99		14098		521		1170		1449		1492		1345		1356		1050		800		1017	

(Continuation)

EXP.	10		11		12		13		14		15		16		17		18		19		20		21	
	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D
I	—	10	—	—	—	12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
II	—	10	—	22	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
III	10	60	—	88	—	48	26	52	28	56	—	45	16	64	17	68	18	18	—	—	—	20	21	21
IV	60	80	66	154	48	24	39	78	—	42	15	45	—	32	17	102	18	54	19	38	—	—	—	—
V	160	230	121	77	36	132	39	91	—	42	15	45	32	80	—	—	18	72	—	38	—	20	—	—
VI	100	100	55	132	48	84	65	78	56	126	45	60	—	—	—	—	18	36	—	—	—	40	—	—
Totals	330	490	242	473	132	300	169	299	84	266	75	195	48	176	34	170	54	144	19	76	—	80	21	21
Grand Totals	820		715		432		468		350		270		224		204		198		95		80		42	

The total number of branches produced in the light and dark cultures in the six experiments and their distribution in the groups based on whorls per plant are given in table 4. A total of 30623 branches were produced and they were distributed about equally between the light and dark cultures (15059, 49.1 per cent, in light to 15564, 50.8 per cent in darkness). The largest number of branches (3467) in any one group is found in that with three whorls per plant. The general trend of the series is similar to that for the numbers of plants and for the numbers of whorls as shown in tables 2 and 3. The largest number of branches in any one group of the light cultures (2474) is also in the group with three whorls of branches. The largest number of branches in the dark cultures (1412) is in the group of plants with six whorls per plant. The number of branches per group is higher in the light cultures than in the dark cultures in the groups with from one to six whorls of branches. In the plants with from seven to twenty-one whorls there are consistently more branches in the dark cultures. There is a consistent excess in the dark cultures from the seventh to the twenty-first group inclusive. The single plant with twenty-one whorls of branches in the dark cultures has forty-eight branches against forty-three branches, for the corresponding single plant with twenty-one whorls in the light cultures. The average number of branches per whorl for all the branched plants studied, as noted above, is 2.11 for the light cultures and 2.23 for the dark cultures (table 1).

Table 5 shows the average number of branches per whorl for each of the six experiments in the successive groups of plants with from one to twenty-one whorls of branches per plant. There is fluctuation in the average number of branches per whorl both in the experiments taken separately and in the relations of the results in the light and dark cultures. The averages for all the groups from one to twenty-one is consistently higher for the cultures grown in relatively continuous darkness. The highest average number of branches per whorl (2.4) is in the group of plants grown in darkness with three whorls of branches per plant. The averages for the five dark grown groups with from two to six whorls are 2.3 or more. The last five groups grown in darkness have averages of about two, except the single plant with twenty-one whorls, which has an average of 2.2 branches per whorl.

In the series of groups grown in alternating day and night the first eight groups have averages of from 2.04 to 2.36 branches per whorl. The highest average 2.36 is, as in the case of the dark grown plants, in the group with three whorls of branches per plant. The remainder of the light cultures in the groups with from nine to twenty-one whorls per plant have

TABLE 4
Branches grouped according to number of whorls per plant

NUMBER OF BRANCHES PER GROUP

EXP.	CULTURES L	CULTURES D	TOTAL BRANCHES L	TOTAL BRANCHES D	1 L	1 D	2 L	2 D	3 L	3 D	4 L	4 D	5 L	5 D	6 L	6 D	7 L	7 D	8 L	8 D	9 L	9 D
I	7	7	864	2097	163	57	307	162	238	321	58	398	61	258	24	473	13	242	—	71	—	72
II	5	4	237	828	57	20	79	102	68	115	5	104	22	65	6	59	—	121	—	101	—	55
III	9	10	2091	2595	55	79	217	181	417	130	284	229	313	150	369	289	151	169	89	136	111	130
IV	9	9	2391	2385	83	49	225	103	334	127	355	110	294	257	199	89	194	215	77	192	128	219
V	10	9	4916	3533	249	55	564	103	764	136	647	243	578	329	507	209	393	182	172	317	236	408
VI	10	9	4560	4126	170	65	483	131	653	164	697	215	514	160	544	293	262	295	219	337	302	445
Totals	50	49	15059	15564	777	325	1875	782	2474	993	2046	1299	1782	1219	1649	1412	1013	1224	557	1154	777	1329
Grand Totals	99		30623		1102		2657		3467		3345		3001		3061		2237		1711		2106	

(Continuation)

EXP.	10 L	10 D	11 L	11 D	12 L	12 D	13 L	13 D	14 L	14 D	15 L	15 D	16 L	16 D	17 L	17 D	18 L	18 D	19 L	19 D	20 L	20 D	21 L	21 D
I	—	22	—	—	—	21	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
II	—	25	—	61	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
III	27	150	—	236	—	125	58	120	—	129	—	105	—	155	—	—	—	—	—	—	—	34	—	48
IV	108	155	130	321	93	57	64	181	46	85	16	111	26	—	19	118	—	40	—	74	—	—	—	—
V	290	487	225	172	57	255	63	186	—	75	18	74	—	50	37	—	41	94	32	—	—	40	43	43
VI	175	228	86	290	77	176	95	164	92	285	73	145	53	167	—	233	55	167	—	80	—	86	—	—
Totals	600	1067	441	1080	227	634	280	651	138	574	107	435	79	372	56	351	96	301	32	154	—	160	43	48
Grand Totals	1667		1521		861		931		712		542		451		407		397		186		160		91	

averages of from 1.42 to 1.95, except in the case of the single plant with twenty-one whorls, whose average is 2.04. There is a tendency for the groups with from one to six whorls of branches to have higher average numbers of branches per whorl. This difference is slightly greater in the cultures grown in alternating day and night, than in those grown in relatively continuous darkness. The possible significance of such data may become more clear in the light of extensive measurements of length of branches, diameters of sori, etc.

For a more detailed study of these light effects we may turn again to the summary given in table 1, where, as also in tables 2–9. the numbers are all based directly on the original data as given by the 50 cultures in light and the 49 cultures in relative darkness. I am noting in the text in certain cases the results given when allowance is made for the difference of one in the number of light and dark cultures in experiments II, III, VI, and in the totals. These differences affect only the evidence as to the degree of the light effects.

As noted, for all six experiments the total number of plants in the cultures grown in alternating daylight and darkness is 2940 as compared with 1569 for the plants grown in relatively continuous darkness. There is an excess of 1371 in the number of plants in favor of the light cultures. In each experiment taken separately the total number of plants produced in the light was greater than that in the darkness.

In experiment III there was one more Petri dish culture in the dark series than in the light series. In experiments II and IV there was one more culture in the light series than in the dark series. The total number of cultures in the light was 50 against 49 in the dark. Allowing for the additional culture in the light, the totals become 2882 plants produced in light against 1569 plants produced in the dark, an excess of 1312 in favor of the light. That is equal numbers of cultures in the light and in the dark produced respectively 64 per cent and 35 per cent of the total number of plants.

The total number of unbranched plants produced in the six experiments was 1379, of which 1025 (74%) were in the light cultures and only 354 (25%) in those grown in relative darkness. There is an excess of unbranched plants in the light cultures of every experiment except the third in which there were 9 cultures in the light and 10 in darkness. If we allow for the difference of one additional culture in the darkness in experiment III the number of unbranched plants becomes 67.5 for the dark cultures, which is 2.5 more than the number in the corresponding cultures grown in light (65). As noted there is also an excess of one each in the number of cultures in light in experiments II and VI. Corrections for the differences

TABLE 5

Average branches per whorl grouped according to number of whorls per plant

EXP.	GRAND AVERAGES		1		2		3		4		5		6		7		8		9		10	
	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D
I	2.3	2.4	2.2	2.2	2.4	2.3	2.4	2.6	2.0	2.6	2.4	2.4	2.0	2.3	1.8	2.3	—	2.2	—	2.0	—	2.2
II	1.9	2.6	2.0	2.2	1.8	2.4	2.2	2.7	1.2	2.3	2.2	2.6	1.0	2.4	—	2.4	—	3.1	—	3.0	—	2.5
III	2.6	2.5	2.5	2.4	2.4	2.5	2.8	2.5	2.7	2.7	2.4	2.5	2.9	3.0	2.3	2.1	2.7	2.8	2.4	2.4	2.7	2.5
IV	2.0	2.2	2.0	2.3	2.2	2.4	2.3	2.4	2.2	2.5	2.1	2.5	1.9	2.1	1.9	2.0	1.9	2.1	1.7	2.2	1.8	1.9
V	2.0	2.0	1.9	1.8	2.2	2.1	2.2	2.1	2.1	2.0	2.1	2.0	2.1	1.9	2.1	2.0	2.1	2.0	1.8	2.1	1.8	2.1
VI	1.9	2.1	1.9	2.4	2.1	2.1	2.2	2.1	2.0	1.9	2.0	2.0	2.0	2.1	1.9	2.1	1.8	1.9	1.8	2.0	1.7	2.2
Averages			2.0	2.2	2.2	2.3	2.3	2.4	2.1	2.3	2.1	2.3	2.1	2.3	2.0	2.1	2.0	2.1	1.9	2.1	1.8	2.1

(*Continuation*)

EXP.	11		12		13		14		15		16		17		18		19		20		21	
	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D	L	D
I	—	—	—	1.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
II	—	2.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.7	—	—
III	—	2.6	—	2.6	2.2	2.3	—	2.3	—	2.3	—	2.4	—	—	—	—	—	—	—	—	—	2.2
IV	1.9	2.0	1.9	2.3	1.6	2.3	1.6	2.0	1.0	2.4	1.6	—	1.1	1.7	2.2	2.2	—	1.9	—	—	—	—
V	1.8	2.2	1.5	1.9	1.6	2.0	—	1.7	1.2	1.6	—	1.5	2.1	2.2	1.5	1.7	1.6	—	2.0	2.0	2.0	—
VI	1.5	2.1	1.6	2.0	1.4	2.1	1.6	2.2	1.6	2.4	1.6	2.0	—	—	—	2.3	—	2.1	—	2.1	—	—
Averages	1.8	2.2	1.7	2.1	1.6	2.1	1.6	2.1	1.4	2.2	1.6	2.1	1.6	2.0	1.7	2.0	1.6	2.0	2.0	2.0	2.0	2.2

in these cases, however, still leave a notable excess in the number of plants in the light cultures.

The average number of unbranched plants per culture in the light series in the data recorded for experiment III was 7.2. In the dark cultures it was 7.5, only a fractional difference in favor of the dark cultures. In the remainder of the experiments the average excess of unbranched plants per culture in the light ranged from 5.4 in experiment IV to 28.3 in experiment I.

The total number of branched plants produced in the six experiments was 1915 in the light and 1215 in the darkness, a total of 3130 (table 1). While there is an excess of branched plants in the light cultures it is by no means so conspicuous as in the case of the unbranched plants. The average numbers of branched plants per culture in light and darkness respectively are 38 in light to 24 in darkness, as compared with 20 in light to 7 in darkness for the unbranched plants. As shown in table I, the average number of branched and unbranched plants per culture taken together is consistently higher in the light in all six experiments. The averages for the total plants in the six experiments are 58 plants in light to 32 plants in darkness.

Allowing for the additional culture in the light the totals are 1004 unbranched plants in light to 354 unbranched plants in darkness. That is 73 per cent of the unbranched plants were produced in the light cultures, against 26 per cent produced in darkness. In the case of the branched plants the difference in their distribution between dark and light cultures is not so marked and is much more irregular. There is an excess of branched plants in the light cultures in four of the experiments, numbers III to VI, while in experiments I and II there is an excess of branched plants in the dark cultures. Allowing for the additional culture in the light series the totals for the branched plants are 1876.7 in the light cultures and 1215 in the dark cultures. That is about 60 per cent of the branched plants appeared in the light cultures to 39 per cent in the dark cultures a difference by no means so marked as in the case of the unbranched plants. It is apparent that for both unbranched and branched plants the ordinary alternation of day and night tends to increase the number of plants per culture as compared with relatively continuous darkness.

Table I also shows the total numbers of whorls and branches produced in the 99 cultures and the average number of whorls per unbranched and branched plant in light and darkness. Taking account of the additional culture in the light series the total number of whorls for the plants grown in light is 6989.3 against 6966 for the plants in darkness, a difference of about twenty-three. That is, of the 13956 whorls produced by 98 cultures, 50 per cent were borne by the plants in the light cultures to 49 per cent

ı the dark cultures. As the table shows, the average number of whorls per ranched plant is consistently higher in each experiment for the plants rown in relative darkness. For all six experiments the average number of ɾhorls per branched plant in the light is 3.72 and in darkness 5.73.

The total numbers of branches in the light and dark cultures, are re- pectively 15059 and 15564, an excess of 1.7 per cent for the plants grown n darkness. Allowing for the extra culture in the light series the totals ɔecome about 14758 and 15564 a grand total of about 30322 branches for ʹ8 cultures of which about 48 per cent were produced in the light cultures ınd 51 per cent in darkness.

The sori can be regarded as forming two groups: (*a*) the terminal sori, ɔf which of course there is one for each sorocarp whether branched or un- ɔranched, and (*b*) the lateral, which are the same in number as the ɔranches. Of the total sori in the 99 cultures of both groups *a* and *b* (35132) ːhere are 51.2 per cent from the light cultures and 48.7 per cent from the lark cultures, an excess of 2.5 per cent in favor of the light cultures. Mak- ːng a reduction of one culture from the light series, the totals of apical sori become about 2882 in light and 1569 in darkness and making similar al- lowance for the extra culture in light in the case of the branches, we have totals of lateral sori of about 14758 in light and 15564 in darkness. The totals for both apical and lateral sori in light and darkness are respectively about 17640 (50.7%) in the light cultures and 17133 (49.2%) for the cul- tures in darkness—a difference of 1.5 per cent in favor of the cultures in light. The problem as to the relative number of spores produced in the light and dark cultures will of course require careful measurements of the size of the sori, etc. The apical sori are regularly larger than those on the branches and as noted my cultures show that relatively more unbranched sorocarps are produced in the light cultures.

The last two columns in table I give the average numbers of branches per plant (5.12 in light, 9.91 in darkness) for all plants including both branched and unbranched plants. This treatment of the unbranched plants as for the most part simply the result of light inhibition, makes more evi- dent the increased proportion of branches produced in darkness. There is a consistent excess in the average number of whorls per branched plant and the average number of branches per plant in the dark cultures in all experiments. This is also true in the average number of branches per plant for all plants both branched and unbranched (table 1) and this latter dif- ference is perhaps a more accurate measure of the influence of light on branching under the conditions prevailing in these experiments. However, it remains to be shown to what degree unbranched plants would disappear from cultures grown in total and continuous darkness.

The data in table 1 indicate that the normal alternation of day and night as contrasted with relatively continuous darkness tends to decrease the average number of whorls and branches per branched plant and increase the number of plants per culture so that the total numbers of whorls, branches and sori are not very different in the light and dark cultures. The average number of branches per whorl for all the branched plants is 2.17. For the branched plants in the light the average is 2.11; for those in the dark it is 2.23 (table 1).

Summarizing the data in table 1 and making an allowance for the additional culture in the light series it is shown that:

49 cultures in alternating day and night produced about:

65% of all the plants
  (a) 73% of the unbranched
  (b) 60% of the branched
50% of the whorls
48% of the branches
50% of the total sori

The 49 cultures in relative darkness produced about:

35% of all the plants
  (a) 26% of unbranched
  (b) 39% of branched
49% of the whorls
51% of the branches
49% of the total sori

The excess of whorls, branches and sori per plant computed for the average plant may be summarized from the data in table 1 as follows. The average plant from the 49 dark cultures had:

(1) 21+% more whorls per average branched plant,
(2) 23+% more branches in the average branched plant, 31+% more branches in the average of all plants, both branched and unbranched,
(3) 28+% more sori per average plant,

than the average plant of the 50 light cultures.

The notable difference in the number of whorls, branches, and hence sori in the average plant from the cultures grown in alternating daylight and darkness, when compared with the average plant from the cultures grown in relatively continuous darkness while the total numbers of whorls, branches, and sori are very much the same for the light and dark cultures, brings out the relation of light to the size of plants as contrasted with number of plants which are formed from a given number of germ cells, and thus differentiates the light relations of growth and cell multiplication on the one hand and architectonic morphogenesis on the other.

The nature of the organization of the sorocarp and the effect of light upon it are further illustrated by classing:

(1) The plants in groups according to the number of branches per plant (table 6A).

(2) The whorls in groups according to the number of branches per whorl (table 6B).

TABLE 6A. *Plants grouped according to the number of branches per plant*

NO. BR.	1		2		3		4		5		6	
	L	D	L	D	L	D	L	D	L	D	L	D
No. Pl.	110	34	187	70	159	59	179	68	171	67	176	63
Per cent	76	23	72	27	72	27	72	27	71	28	73	26

(Continuation)

NO. BR.	7		8		9		10		11		12	
	L	D	L	D	L	D	L	D	L	D	L	D
No. Pl.	126	68	130	58	114	68	69	54	67	55	75	51
Per cent	64	35	69	30	62	37	56	43	54	45	59	40

(Continuation)

NO. BR.	13		14		15		16		17		18	
	L	D	L	D	L	D	L	D	L	D	L	D
No. Pl.	61	38	44	41	46	34	31	43	32	40	20	31
Per cent	61	38	51	48	57	42	41	58	44	55	39	60

(Continuation)

NO. BR.	19		20		21		22		23		24	
	L	D	L	D	L	D	L	D	L	D	L	D
No. Pl.	24	20	23	28	15	15	8	26	11	26	9	15
Per cent	54	45	45	54	50	50	23	76	29	70	37	62

(Continuation)

NO. BR.	25		26		27		28		29		30	
	L	D	L	D	L	D	L	D	L	D	L	D
No. Pl.	7	11	4	12	3	21	3	10	1	9	2	11
Per cent	38	61	25	75	12	87	23	76	10	90	15	84

(Continuation)

NO. BR.	31		32		33		34		35		36		37	
	L	D	L	D	L	D	L	D	L	D	L	D	L	D
No. Pl.	2	8	1	5	1	12	1	4	—	2	—	3	1	6
Per cent	20	80	16	83	7	92	20	80	—	100	—	100	14	85

(Continuation)

NO. BR.	38		39		40		41		42		43		44	
	L	D	L	D	L	D	L	D	L	D	L	D	L	D
No. Pl.	—	4	—	—	—	5	1	1	—	4	1	3	—	3
Per cent	—	100	—	—	—	100	50	50	—	100	25	75	—	100

(Continuation)

NO. BR.	45		47		48		49		51		54		56	
	L	D	L	D	L	D	L	D	L	D	L	D	L	D
No. Pl.	—	2	—	1	—	2	—	1	—	1	—	1	—	1
Per cent	—	100	—	100	—	100	—	100	—	100	—	100	—	100

As shown in table 6A, the number of branches per plant ranges from one to fifty-six. The group with two branches has the largest number of plants (257). This group also has the highest number of plants (187) in the light cultures. The highest percentage of plants is found in the group with only one branch per plant, 76 per cent in the light and 23 per cent in the dark cultures.

The percentage relations of the numbers of plants in the light and dark cultures when classed by the number of branches per plant show a striking uniformity in the first six groups, that is, the groups with respectively from one to six branches per plant. From the sixth group on the percentage of plants in the light tends to diminish but is in excess of the plants in darkness till the sixteenth group is reached, where the dark plants become relatively more numerous. No plants with more than forty-three branches appeared in the light cultures, and of these there was but one. This plant was one of three in the light cultures which had more than thirty-four branches, while in the dark cultures forty plants had more then thirty-four branches each. The largest number of branches in a single plant was, as noted, fifty-six. One plant each had forty-nine, fifty-one, fifty-four, and fifty-six branches, as shown in the table. The data in table 6A illustrate again the appearance of large numbers of plants with very few branches in the cultures as I have grown them, and must not necessarily be regarded as typical of the plants as they occur in nature.

There is a conspicuous excess of plants in the light cultures which extends to the group with fifteen branches, in which the numbers are forty-six plants in light to thirty-four in the dark cultures. From this point on the larger numbers of plants are consistently in the dark cultures, with two exceptions—the group with nineteen branches, which consists of twenty-four plants in the light to twenty in the dark and the group with twenty-one branches, in which the numbers of plants in the light and dark cultures are equal (fifteen).

The transition from the one distribution to the other comes in the region of the groups with from fifteen to twenty branches which may be taken in such a classification as the region of the typical plant, as grown in inverted Petri dish cultures, with five or six whorls of about three branches each,—possibly two branches in the first whorl, four branches in the apical whorl, and three or four intermediate whorls of three branches each. If the light is increased there will be a tendency to diminish the number of whorls and branches per plant. If the light is diminished there will be a tendency to increase the number of whorls and branches per plant. The average number of branches per plant in such a branched type is 7.8+ in light and 12.8+ in darkness (table 1).

One half of the total number of branched plants (1515) is included in the groups having from one to about seven branches per plant. One-half the total number of branches (15311) is found in the groups having from one to about six whorls of branches per plant (table 4). Including the light cultures of the group with six whorls gives 15221 branches.

When the branches are classed according to the number per whorl (table 6B) the group with a single branch per whorl is the largest (4512, thirty-two per cent) but the variation is not great till we pass the group with three branches per whorl, which totals for the light and dark cultures together 3960 (twenty-eight per cent). The group with four branches per whorl includes only nine per cent of the total. The groups with five and six branches per whorl each include less than one per cent of the total number of whorls. There are but six cases of whorls with six branches each. It is to be remembered here also that, as stated, the branches in such whorls are very likely not to be at exactly the same level on the stipe. In many cases the plants in such a group might almost better be classed as having whorls of four or five branches with an accessory branch or whorl of one branch standing slightly above or below the whorl. The distribution of the classes based on number of branches per whorl illustrates very well the nature of mixed classifications in which the individual cases in a series are determined by very different factors.

The whorl of three branches is perhaps to be regarded as the normal type, giving a compact arrangement of the cleavage sectors of the segmental mass as it divides. However, the fact that, as shown in table 6B, whorls with one, two, and three branches each tend to be fairly equal in number indicates that no very fundamental physical principle determines the cleavage of the segmental mass, nor perhaps its size as it abstricts itself from the sorogenic mass. Measurements of the length of the branches and the diameter of the sori in their mutual inter-relations and in their relation to the number of branches in the whorl may throw more light on the questions here involved.

The proportion of whorls of plants having respectively one and two branches each (32%, 29%) is about the same as the proportion of un-

TABLE 6B

The whorls grouped according to the number of branches per whorl

NO. OF BR.	1		2		3		4		5		6	
	L	D	L	D	L	D	L	D	L	D	L	D
	2390	2122	2203	2009	1948	2012	540	431	49	88	2	4
Total	4512		4212		3960		1271		137		6	
Per cent	32		29		28		9		.9		—	

branched plants (30%). When the plants are classed according to their number of branches the largest single group is, as noted, that with only two branches per plant as shown in table 6A.

METAMERISM AND TAPER

The evidence as to variation in the number of branches per whorl, when considered from the standpoint of the groups of plants based on the number of whorls per plant, has been given above and the tendency to higher numbers of branches per whorl in the groups of plants with smaller numbers of whorls per plant (6–10; table 5) was noted. These data do not, however, show whether in the individual plant such variations in the numbers of branches per whorl tend to be so distributed from base to apex of the plant as to result in a metameric taper. The figures of *Polysphondylium* commonly given in books of reference, and based on those of Olive and Brefeld, show prounounced taper from base to apex. As bearing on this question, the plants with three or more whorls were taken as a group which show basal and apical whorls and at least one intermediate whorl in which the number of branches per whorl can be compared. The distribution of basal, intermediate, and terminal whorls and branches is given in table 7. The plants with one or two whorls per plant were classed separately as a group in which metamerism is so slightly in evidence that a tendency to tapering could hardly come to expression.

The size of the nodal mass as abstricted from the sorogenic mass is doubtless a factor in determining the number of branches in a whorl, as noted, but the relation of length of branch and size of sorus to number of branches per whorl must be taken into account. Assuming that the segments abstricted are about the same in length, the size of any one of them will depend on the diameter of the sorogenic mass. If for any reason the sorogenic mass becomes more elongated and thinner the size of the nodal masses will be less and the number of branches per whorl will probably tend to be smaller. It is possible with suitable culture apparatus to grow the plants under conditions which will make it possible to photograph them at each successive stage in their development so that length and diameter of any nodal segment, and number and dimensions of each branch and sorus formed from it can be more or less accurately determined.

By varying the light, temperature, moisture, and other conditions it will be possible to determine whether and to what degree these dimensional relations can be modified by environmental changes. Studies bearing on such data are under way and I shall hope to report the results later. At present we are concerned with the evidence as to taper in sorocarps grown under the conditions above described.

The relative number of branches per whorl from base to apex of the sorocarp was determined for a group consisting of 2024 plants, each having as noted, three or more whorls per plant (table 7). The whorls were grouped according to their position as basal, intermediate, and terminal. The data as given show that the average number of branches in the apical and basal whorls of the plants in both light and dark cultures is slightly different than for the intermediate whorls. The average number of branches in the terminal whorl of all plants having three or more whorls of branches is 2.44 in the light and 2.45 in darkness. The average number for the basal whorl is 1.71 in the light and 1.69 in darkness, and for the intermediate whorls it is 2.10 in the light and 2.28 in darkness. There is thus shown perhaps a slight tendency for the top whorl to have more branches and the

TABLE 7

Distribution of whorls and branches in plants with three or more whorls

	TOTALS									
EXP.	BASAL				INTERMEDIATE				TERMINAL	
	NO. OF PLANTS		BRANCHES		WHORLS		BRANCHES		BRANCHES	
	L	D	L	D	L	D	L	D	L	D
I	47	157	98	324	74	456	180	1163	116	391
II	14	50	28	103	22	166	44	468	29	135
III	143	124	326	235	397	676	1103	1771	390	329
IV	183	131	283	210	675	746	1361	1688	439	335
V	372	218	596	316	1245	1238	2616	2569	891	490
VI	360	225	588	347	1266	1398	2450	3039	869	544
Totals	1119	905	1919	1535	3679	4680	7754	10698	2734	2224
Grand Totals	2024		3454		8359		18452		4958	

(Continuation)

	AVERAGES									
EXP	BASAL		INTERMEDIATE		TERMINAL		WHLS. PER PL. FOR BR. PLS.		BRS. PER WHORL	
	L	D	L	D	L	D	L	D	L	D
I	2.0	2.0	2.4	2.5	2.4	2.4	2.0	3.9	2.3	2.4
II	2.0	2.0	2.0	2.8	2.0	2.7	1.9	3.9	1.9	2.5
III	2.2	1.8	2.7	2.6	2.7	2.6	3.7	5.3	2.6	2.5
IV	1.5	1.6	2.0	2.2	2.3	2.5	4.3	6.1	2.0	2.2
V	1.6	1.4	2.1	2.0	2.3	2.2	3.7	6.4	2.0	2.0
VI	1.6	1.5	1.9	2.1	2.4	2.4	4.0	6.8	1.9	2.1
Average	1.71	1.69	2.10	2.28	2.44	2.45	3.7	5.7	2.1	2.2

basal whorl to have fewer branches than do the intermediate whorls in plants with three or more whorls. Table 7 shows also the distribution in the six experiments of the average numbers of whorls per plant (3.7 in light and 5.7 in darkness) and of branches per whorl, for all branched plants, (2.1 in light and 2.2 in darkness). The average number of branches per plant for the whole series is 5.1 for the light cultures and 9.9 for the dark cultures (table 1). The average number of branches per whorl for all branched plants is 2.17, which is close to the average for the intermediate whorls (2.19; table 7).

The differences in average number of branches between basal, intermediate, and apical whorls do not hold consistently for each of the six experiments taken separately. Nor do the same relations hold for the cultures in light and darkness taken separately. There is no conspicuous evidence from the plants in these cultures that the sorocarp as a whole tapers either up or down, though there is the slight indication given in the table that the number of branches per whorl tends to increase slightly from base to apex. It is to be remembered that, as noted, the cultures were all grown in the inverted position and that the illumination was not equal on all sides. Experiments controlled for this particular purpose are needed to show definitely whether there is any evidence of taper either up or down.

The data as to the distribution of whorls and branches in the remainder of the branched plants, namely, those with one or two whorls of branches, are given in table 8. The total number of plants in these two groups, taking the fifty light cultures and the forty-nine in darkness is 1106, a little over one-third of the total number of branched plants (3130). There are over twice as many plants with one or two whorls per plant in

TABLE 8

Distribution of branches in plants with one or two whorls per plant

EXP.	PLANTS		TOTALS PER EXPERIMENT				AVERAGES			
			WHORLS		BRANCHES		BR. PER WH.		BR. PER PL.	
	L	D	L	D	L	D	L	D	L	D
I	133	59	195	93	470	219	2.4	2.3	3.5	3.7
II	49	30	70	51	136	122	1.9	2.3	2.7	4.0
III	66	68	110	104	272	260	2.4	2.5	4.1	3.8
IV	91	42	142	63	308	153	2.1	2.4	3.3	3.6
V	255	54	383	78	813	158	2.1	2.0	3.1	2.9
VI	202	57	315	87	653	196	2.0	2.2	3.2	3.4
Totals	796	310	1215	476	2652	1108	2.1	2.3	3.3	3.5
Grand Totals	1106		1691		3760					

the fifty light cultures as there are in the forty-nine cultures in darkness. Experiment III is the only one which shows an excess of plants of this type in the dark cultures and in this case, as the table shows, there were nine light cultures to ten dark cultures. If we allow for this difference the numbers of plants in this experiment also show an excess in the light—sixty-six in light to about sixty-two in darkness. This excess of plants in the light cultures, which is so marked in the group of plants with one and two whorls of branches, gradually decreases (as shown in table 2), till in the group of plants with seven whorls of branches there are more plants in the dark cultures than in the light (69L to 81D). In the case of the numbers of whorls and branches there is a consistent excess in the light cultures over the dark cultures in the case of the groups of plants with one and two whorls of branches each.

The average number of branches per whorl for these plants is 2.1 in the light to 2.3 in the dark (table 8), about the same as for the intermediate whorls in the plants with three or more whorls (2.1 and 2.2; table 7). The average number of branches per plant is 3.3 in light to 3.5 in darkness. These averages of branches per whorl and branches per plant in plants with one or two whorls are both consistent with the evidence that light tends to inhibit the branching of the plants.

The relation of light to number of plants produced is further illustrated in tables 7 and 8. In the columns showing total plants in the light and darkness respectively of the two groups, those with three or more whorls per plant and those with one or two whorls per plant, we find that: in the first group (table 7) 55+ per cent of the plants are in the light cultures to 44+ per cent of the plants in the dark cultures. While in table 8 71+ per cent are shown to be produced in the light to 28 per cent in darkness.

EXTREME DIVERGENCES FROM TYPE

A study of the data indicates that extreme divergences from type can occur in the organization of the sorocarp, and that symmetry in the distribution of the whorls and branches may be present or lacking in varying degrees. I have brought together data as to a number of such extremes in total whorls and branches and number of branches per whorl in table 9. Plants with very large numbers of whorls and branches (table 9A 1, 2, 3) may show great irregularity in the distribution of the numbers of branches per whorl. I have noted the slight tendency to smaller numbers of branches in the basal whorl of sorocarps with three or more whorls of branches. A very considerable number of plants have basal whorls of one branch. In plants A1, 3, and B3, and to a lesser degree in B1 and 2 (table 9) this tend-

ency comes to extreme expression. From four to ten of the lower whorls consist of a single branch each. The average numbers of branches in the basal whorls of plants with three or more branches are 1.7L and 1.6D (table 8).

TABLE 9

Plants showing extreme divergences from type in numbers of whorls and branches per whorl
A. Plants with high numbers of whorls and branches

EXP.	CULT.	
V	607	1. Plant in light with highest no. of branches; has 21 wh. 43 br. *1 1 1 1 1 1 1 1 1 2 1 1 3 2 4 3 4 3 4 3 4 This is also the plant with the highest no. of whorls.
VI	628	2. Plant in dark with highest no. of branches; has 17 wh. 56 br. *1 1 4 5 2 3 4 3 3 4 5 4 4 4 3 3 3
III	460	3. Plant in dark with highest no. of whorls; has 21 wh. 48 br. *1 1 1 1 1 1 1 1 1 1 2 3 3 4 4 4 3 4 4 3 4

B. Plants with a whorl of six branches

III	465	1. Plant in dark with 15 wh. and 28 br. av. br. per wh. 1.8 *1 1 1 1 2 3 3 2 2 1 1 2 6 1 1
III	466	2. Plant in dark with 10 wh. and 23 br. av. br. per wh. 2.3 *1 1 1 1 1 2 3 6 4 3
III	465	3. Plant in dark with 16 wh. and 30 br. av. br. per wh. 1.8 *1 1 1 1 1 1 1 3 3 2 1 3 1 1 3 6
V	617	4. Plant in dark with 10 wh. and 32 br. av. br. per wh. 3.2 *1 2 3 4 2 3 6 4 4 3
III	456	5. Plant in light with 6 wh. and 24 br. av. br. per wh. 4.0 *2 2 4 5 6 5
IV	491	6. Plant in light with 4 wh. and 14 br. av. br. per wh. 3.5 *4 3 6 1

* The order is from base to apex of the plant.

Plants A1 and 3 have apical whorls of four branches, as well as being respectively the plants with the largest total number of whorls in the light and dark cultures. Plant B3 has an apical whorl of six branches. In the other plants of group B (table 9) the whorls with six branches are intermediate. The average apical whorl for all plants with three or more whorls is 2.44L and 2.45D (table 7). The average apical whorl for the four specially selected plants, B2, 3, 4, 5, is 4.25 branches. Plant A2 with 17 whorls and the highest number of branches of any plant observed (56) has its two lowest whorls with one branch each and an apical whorl of three branches.

Its intermediate whorls consist of one with five branches, six with four branches each, five with three branches each, and one with two branches, average 3.4. The average intermediate whorl for all plants with three or more whorls is 2.10L, 2.28D.

I have noted the doubtful nature of the whorls with six branches. The six plants B1, 2, 3, 4, 5, and 6 which showed such whorls range in total number of whorls from 4 to 16. The average number of branches per whorl for the group is about 3 (3.8L and 2.2D). The average for all branched plants is 2.11L, 2.23D (table 1).

Plants with only one branch are found in all of the six experiments (table 6A). There is a total of 110 such plants in the light cultures to 34 in the dark cultures. Such plants come nearest to *Dictyostelium* in their organization and their predominance in the light cultures suggests that the transition from unbranched to branched types is favored by development in darkness.

In comparing such data as the above with similar data for types in which growth and differentiation go on simultaneously it is to be remembered that in these pseudo-plasmodial plants, relative size of the plants, number of whorls, and number of branches in a whorl are determined solely by building, architectonic processes of aggregation, integration, and differentiation and not at all by the regulation of cell growth and cell division. The data indicate that the stimuli which determine the size of the sorocarps operate by regulatory effects determining the area from which the myxamoebae come together to produce a single plant body. These extreme cases of asymmetry in the distribution of whorls, branches, and branches per whorl emphasize the complicated nature of the processes by

which the morphogenesis of so simple a plant form as the sorocarp is achieved, but in no way invalidate the evidence that normal alternation of day and night tends to favor the production of more and smaller plants, while relatively continuous darkness tends to the production of larger and fewer plants. This would indicate again, as noted, that cell growth and division go on equally well under both sets of conditions but that the regulation of aggregation and architectonic morphogenesis is such as to tend in darkness to favor the gathering of larger numbers of myxamoebae at each point of integration, thus resulting in the formation of fewer and larger plants per unit culture.

DISCUSSION

Growth. The general results of these experiments indicate a fixity of type in *Polysphondylium* under varying environmental conditions which parallels that in ordinary cormophytic plants. Environment may alter

size, but the type configuration persists. The experiments give further data as to the nature of this type configuration and the range in variation of *Polysphondylium*, and show the general relations of light to its processes of growth, integration, and differentiation.

That free motile cells may, by strictly architectonic or building processes, as contrasted with cell division and cell growth, develop highly specialized and symmetrical organic forms is clear, and that both environmental and hereditary variants are to be found in such types emphasizes the fundamental identity of their morphogenetic processes with those in plants whose cells are in more persistent continuity.

The Acrasieae are very simple plants, and it may perhaps be questioned whether their erect stems and whorls of branches bearing fruiting organs, the sori, justify any comparison with the superficially similar structures of the higher plants. There can be no question, however, that we have here a case of the formation of well differentiated multicellular plant forms in which cell growth and nuclear and cell division are sharply separated in time from the integrating and differentiating processes which result in the formation of the erect radially and metamerically symmetrical plant body. In such a life cycle we can study this integrating and differentiating phase in entire independence of the equally complex processes of cell growth and cell multiplication. This morphogenetic phase involves what is, to use the familiar illustration, essentially an architectural and building process as distinct from the manufacture and accumulation of building materials. It is architectonic in that it is not merely aggregative but involves the production of hereditarily specified plant forms which require for their development characteristic and progressively changing relations of the amoebae to each other and to the external environment quite as in the development of the embryonic cells into the organs and tissues of the mature many-celled plant following the cleavage of the egg. The process is essentially a morphogenesis, but we may characterize it more specifically as an architectonesis, as distinguished from the processes of mass growth and proliferation of cells and undifferentiated cell aggregates, which are also in a sense morphogenetic. It involves both individuating and differentiating processes by which a swarm of isopotential myxamoebae becomes a complex whole comparable to a minute pine tree in its general appearance, and in which the amoebae become ultimately differentiated into organs and tissues, though for a long time maintaining their harmonic equipotential characteristics both singly and as groups.

This organization so achieved is also, as noted above, genetically fixed, and we have a whole series of genera and species in the Acrasieae which seem quite as persistent in their heredity as are plants whose cells are in

ore permanent tissue continuity. I have found no reason to doubt that *ictyostelium* and *Polysphondylium* are genetically distinct, though the ꞏbranched forms of *Polysphondylium* are so similar to *Dictyostelium* in ꞏeir general plan and appearance.

That the architectonic phase in development is distinct and specific very clearly shown in the results of so-called tissue culturing and translantation as developed by the Carel and Spemann schools. Just why the ꞏells of a bit of chick embryo should maintain cell growth and cell prolifration indefinitely and show little or no tendency to form tissues, or orans, or an entire chick, while a bit of hydra so readily undergoes morꞏhallactic individuation, and the cells of a bit of begonia leaf not only ꞏrow and divide but integrate and differentiate into a complete begonia ꞏ, of course, as yet not all clear. The much more successful, though freꞏuently bizarre, development of tissue or organ transplants indicates, ꞏowever, that the processes involved are all in their nature, in part at ꞏeast, intercellular space and chemical hormonic relations. I have discussed ꞏhese relations more fully in connection with the reactions involved in ꞏtipe formation (1929, 1926). But however such integrations and differꞏntations are to be explained, the results so far obtained with tissue culꞏures make very plain the distinction between cell growth and proliferaꞏion and the integrative and differentiating processes by which a mass of cells becomes a unit organism with differentiated organs and tissues, and it is this distinction which is so clean cut in the life cycle of these semicoenobes.

In *Polysphondylium* the stages of growth on the one hand, and of integration and differentiation on the other, almost, as it were, constitute an alternation of generations, so sharply are they separated both as to time and the nature of the processes involved. Still the basic process in building the sorocarp is amoeboid cell motion quite like that occurring while growth and division are going on, but highly determinate and specified cell motion as contrasted with the wanderings of the myxamoebae at the earlier period, though perhaps no less environmentally controlled if we take into account the intercellular environment.

Tropisms. I have referred the direction of anallactic development to such stimuli, as light, gravitation, moisture, etc. Olive (1902) and Potts (1902) have noted a tendency of the pseudoplasmodium to grow away from the substratum under conditions where the orienting factor or factors are not clear. In certain cases I have noted such phenomena under conditions which also certainly need further study. I have frequently observed plants in an inverted Petri dish dung agar culture which had built down vertically forming branches as usual till they reached the glass cover

of the dish, and then have turned and built almost vertically back up-
wards from the glass (exotropy). The glass seemed quite dry. There was
no evidence of negative hygrotropism. The reversed stipe shows no
branches till it has reached something like the length of the basal segment
generally. Though similar, such cases are not to be confused with those in
which a plant lops over until the developing sorogen touches the nutrient
substratum and then changes its direction of anallactic advance until it
regains a position more nearly vertical to the substratum. This may be an
ordinary hygro-geotropic response. In the special cases here referred to the
sorogenic mass reverses its direction of motion on contact with a glass
surface toward which it had just before been advancing.

Types. On the assumption that *Polysphondylium* tends to produce a
certain type of plant as to number of whorls, distance between whorls,
angle of deviation of branches, number of branches per whorl, etc., the
total number of branches, for example, for each group of plants with in-
creasing numbers of whorls (table 4) should increase till the type number
is reached. This is true as shown by the data given in the table, and it
would appear that the type plant has about three or four whorls of
branches with between two and three branches per whorl. Above this type
the total number of whorls or branches per group should and does de-
crease, with a decrease in the number of plants.

The data indicate that the stimuli which determine size and form must
operate as noted by regulatory effects, either determining the extent of the
area from which the amoebae come together to produce a single sorocarp
or their abundance in any given area of the nutrient substratum. The fact
that normal alternation of day and night tends to favor the production of
more and smaller plants while relatively continuous darkness tends to the
production of larger and fewer plants, may be taken to indicate that cell
growth and division go on equally well under both sets of conditions but
that the processes of aggregation and integration tend probably in dark-
ness to favor the gathering of the myxamoebae from larger areas to the
points of integration, thus resulting in the formation of fewer and larger
plants per unit culture.

Photomorphosis. As noted, Potts (1902) has observed that light tends
to reduce the size of the plants of *Polysphondylium*, and he gives the height
of the tallest he obtained in light as 6 mm., with three or four branches,
and in darkness as 13 mm., with twelve branches. He thus leaves the prob-
lem of light effects on growth without discussing the question as to whether
it is a matter of relative cell proliferation or cell aggregation or both. Potts
also gives a mass of data as to the symbiotic, temperature, moisture, and
other relations of these plants. All of these relations, however, have to do

more especially with nutrition and growth, rather than the morphogenetic processes with which my studies are especially concerned, and I shall hence not discuss them further in this connection. Of particular interest are his observations on the effect of an optimum rate of transpiration on the height of the plants.

Stameroff (1897) finds that the vegetative hyphae of *Mucor* and *Saprolegnia* grow equally well in light and darkness, while light tends to check the growth of the fertile hyphae of *Mucor*. It will be interesting to know whether the upward so-called growth of the fertile branches of *Mucor* involves nuclear division and increase in dry weight, or merely the well known streaming of protoplasm from the vegetative hyphae into the reproductive branches. In the latter case the differential effect of light on growth vs. building processes would be the same for *Mucor* as I have found it for *Polysphondylium*.

The observed numerical data for the 50 cultures grown under conditions of alternating day and night, and the 49 cultures grown in relative darkness, are summarized in table 1, and the results obtained, when allowance is made, for the extra culture in light, are given on page 16. The evidence shows that, as Potts discovered, the plants grown in darkness are larger. However, it is also shown that the number of plants is greater in the cultures grown in alternating day and night, so that the total numbers of whorls, branches, and sori produced are about the same. There is a difference of only from one to two per cent (p. 16), while in the number of plants there is a difference of about 29 per cent in favor of the cultures grown under conditions of alternating day and night. The cultures in the light produced 64 per cent of the total number of individual plants, against 35 per cent produced by the cultures in the dark. But the 35 per cent of the plants in the dark produced practically the same percentage of the total number of whorls (50%L, 49%D), branches (48%L, 51%D) and sori (50%L, 49%D) as the 65 per cent of the plants in the light (p. 63).

The percentage of terminal sori, as compared with lateral sori, is greater in the light than in darkness by about 7 per cent owing to the relatively larger number of unbranched plants and those with few branches. The terminal sori of branched plants are larger in general than the lateral sori. I have no data as to the relative diameters of the terminal sori of unbranched plants. Whether the ratio of spores to stipe and branch cells (germ cells to somatic cells) is greater in the unbranched or the branched plants—in the plants grown in light or in darkness—must be determined by further quantitative studies.

The difference between the number of unbranched plants (*Dictyostelium* type) in the light (1025, 74%) as compared with those in the dark

(354, 25%) is (671, 48%). That is, there is an excess of unbranched plants in light of 48 per cent. The difference in the number of branched plants in the light (1915, 61%) and the branched plants in darkness (1215, 38%) is 700 (22 per cent). That is, there is an excess of only 22 per cent of branched plants in the light. It would appear that under the conditions of my experiments, the production of wholly unbranched *Polysphondylium* plants (*Dictyostelium* type) is favored more than twice as much in the light as is the formation of branched plants. This does not, of course, prove that all unbranched plants could be made to disappear by growing the cultures in absolute darkness.

The fact that fungi respond to environmental stimuli of light, heat, chemical conditions of nutrition and stimulation, etc., in highly specific fashions both as to form, rate of development, kind and time of fructification, etc., has long been recognized, and latterly the effects of nutritive and chemical stimuli in producing form changes, so called mutations, has become a subject of special interest. That light particularly has specific and very various effects on the development of the fungi, though unlike green plants they are quite incapable of using it directly as a source of energy in their metabolism, was early noted. The earlier data have been well summarized and analyzed by Elfving (1890), who interested himself especially with the comparison of these light effects in fungi with the phenomena of etiolation in green plants. Zopf in Schenk's *Handbuch* (1890) also brings together the results of Wettstein (1885, p. 39), Klein (1885), Brefeld (1889), Winter (1874), Kraus (1869), and others on the light relations of the fungi. The photomorphotic relations of the higher fungi particularly are extremely varied and frequently bizarre to a degree hardly equalled in the etiolated forms of green plants. Just why a certain species, *Pilobolus oedipus*, can go through its whole life cycle quite normally in darkness, while another, *P. microsporus*, is entirely dependent on light at certain stages (Brefeld, 1889), is as yet quite as little understood as is the whole matter of the effect of light on growth rates in green plants. As, however, the observations of the authors cited for the most part do not extend to an attempt at analysis in terms of cell behavior, I shall not refer to them further at this time than to point out the attractive nature of this field for further study.

Heredity and morphogenesis. The intensive study of the germ plasm and the results achieved by genetical analysis have led naturally, as pointed out by Sinnott, to the effort to trace the direct relations of the germ plasm to the development of the characters of the adult plant. Sinnott and Durham (1929) find that fruits of cucurbits of various shapes and sizes all have cells of the same shape and size. This confirms the work of

Amelung (1893) on the relation of cell size to organ size, and that of Tenopyr (1918) on cell form as related to organ form.

However, in this very careful and critical study of the development of form the authors note that, while the shape of the cells tends to be essentially the same (p. 418) in mature elongate, rounded, and disk shaped fruits, in certain tissues—'inner tissue continuous with the carpellary folds' and 'outer layer'—the cells are respectively 'elongated longitudinally and elongated tangentially' in a fashion which may well indicate directions of cellular mass growth. This suggests that while the form of the mature cell is so to speak standardized independently of fruit form, the growth axes of elongation by which the specific form of the fruit is achieved may be indicated by the form of the cells. It also suggests further that the orientation of the division planes (census growth) may follow rather than precede the determination of the axes of mass growth of the cells.

It is such facts as these which might lead to the conception that mass growth is quite independent of cell division, which may then be assumed to follow in accord with the simple Sachsian principles of rectangular intersection, least surfaces, etc. However, the cell can divide successfully whether it is isodiametric or elongated. It can grow for a time at least equally well either in three dimensions or in one dimension. The cell may show specific inherited characteristics, both as to plane of division and axes of growth enlargement. These relations are amply illustrated in the growth and multiplication stages of the myxamoebae and other types of amoebae, swarm spores, and protophytes generally. The plane of cell division may be controlled by external environmental factors of light, gravity, etc. The direction of movement of free cells or the direction of elongation of attached swarm spores may also be very easily controlled by external environmental stimuli of light, heat, chemical agents, etc.

When such free cells are aggregated in the tissues and organs of many celled plants or animals the new factors which appear are intercellular relations of contact, pressure, chemical stimuli, etc., and it is natural to conclude that these new internal environmental factors, with those of the external environment, have much to do in determining the form and internal functional interrelations of the cells of the multicellular organism, that is, with both individuation and differentiation. That any further principle of organic protoplasmic unity appears in multicellular organisms as such, remains to be proven.

In the architectonic processes of coenobes and semi-coenobes the axial differentiation of the stipe and branches are seen directly to be matters not of protoplasmic mass growth but of specifically oriented movements of independent cell units, the resulting form of the whole being deter-

mined by their coordinated and integrated behavior. Sinnott's (1929) careful observations show clearly that at the critical steps in fruit morphogenesis the specificity of cell form comes to expression even though the specific shape of the mature fruit is in no particular determined by the shape of its cells. Speaking of the development of the ovary wall he says:

Certainly in many cases a rather definite line is visible in early stages of the ovary, between an inner tissue, clearly continuous with the carpellary folds and consisting chiefly of cells *elongated longitudinally*, and an outer layer in which most of the cells are *elongated in a tangential direction*.

These are apparently growth directions indicated directly in the form of the cells and achieved by them in their mutual interrelations. The fruit, as Sinnott shows, is from a very early stage a tissue aggregate consisting of (1) epidermis, (2) cortex, (3) vascular ring, (4) medulla, (5) sterile carpellary tissue, and (6) ovuliferous carpellary tissue. Each such tissue consists of cells of more or less specific shapes which suggest axes of differential elongation analogous to those in amoeboid form changes of specific types.

It is obviously the cellular organization which makes possible all this tissue differentiation. The problems of morphogenesis include all of these interior as well as the more external form specificities and their existence marks very sharply the advance from the architectonic possibilities of the true plasmodium and coenocyte to the complexities of histogenesis and organogeny in the higher plants.

The existence of such architectonic processes as are found in the semi-coenobes *Dictyostelium* and *Polysphondylium* with their pseudoplasmodia of free independent amoeboid cells certainly suggests that the evolution of morphogenetic processes consists in the development of progressively more specific aggregations and integrations of cells rather than in the growth and differentiation of a plasmodial protoplasmic mass whose form, aside from postulated internal form determining tendencies, must be achieved by the surface relations of a single continuous plasma membrane. Sinnott (1922, 1927) emphasizes that the factors which control morphogenesis in cucurbits are not mass or dimensional factors but are essentially factors determining the form, i.e., the *distribution* in space of the unit products of cell growth and multiplication. The differences between a Fordhook and a disk fruit are essentially matters of the distribution of a given number of cells of essentially equivalent form and size. The problems of morphogenesis become thus matters of cell movement and distribution quite as they are in *Polysphondylium*.

Growth hormones. The relations of light to growth have been the subject of very intensive experimentation in recent years. Following the determination of the localization of receptive and motor regions has come

the discovery of the nature and the means of transmission of stimuli from the specially sensitive apex to the elongating motor regions. Went's (1927) demonstration of so-called growth stuff as the product of stimulation and the agency of its transmission has brought the phenomena of phototropic bendings into line with the hormone theory of secretory and growth control in animals. Went's use of the term growth stuff rather then hormone emphasizes the closeness with which the problems of growth and tropistic bending have been interrelated in the minds of students of the light relations of plants. As I have pointed out (1929) *Polysphondylium* shows characteristic and typical tropistic curvatures without either mass growth or cell multiplication being involved in any way. The phenomena are directly tropomorphotic rather than, as generally described, growth curvatures, the stimuli being apparently those of negative hygro-geo- and perhaps exo-tropy. The familiar cases of so-called tropistic growth curvatures in root and shoot apices may be interpreted as matters of oriented amoeboid elongation of the cells in the stretching region back of the apex. This tissue elongation it is agreed is a matter of vacuolization of the cells without necessary increase in dry weight, and it is of great interest that Olive (1902) emphasizes the enlargement by vacuolization of the myxamoebae as a factor in the building of the stipe tissue. In the upturning sorogen of *Polysphondylium* after contact with the substratum the curvature is as noted (1929) strictly due to the tropistic change in direction of movement of each one of the mass of creeping myxamoebae.

Noll, following Godlewski (1879) and others, claimed to demonstrate experimentally that such bending is due to the greater elongation of the cells on their convex flanks resulting from the increased elasticity of the cell walls on that flank. Went (1928) accepts this earlier theory of the unequally changed elasticity of the cell flanks as a mechanical basis of the bending process. Others have claimed that turgor differences between the cells on the two flanks of the bending shoot are involved. However that may be, it seems to me plain that in both *Polysphondylium* and the higher plants the curvature is not a growth process either in the sense of cell multiplication, which I have called census growth, nor in the sense of increase in volume or dry weight of the protoplasmic mass involved. What is common to both cases is specifically oriented cellular protoplasmic motion. In *Polysphondylium*, as noted, a tropistic change in the relative rate of creeping movement of the individual amoebae on the two flanks of the sorogen is the means by which the upward curvature is achieved.

The evidence that certain regions or tissues in the embryo serve as centres for the control of morphogenetic processes as developed by Spemann (1923) and others seems well established. That the root tip and

other embryonic regions in the higher plants function as special receptors was pointed out by Charles Darwin (1880) and has been many times confirmed. Went (1927), as noted, has recently obtained evidence that this control in the coleoptile of the oat is effected by the formation and migration to motor regions of what he calls growth stuff. Pincussen (1930), in his valuable and interesting analysis and summary of the light relations of organisms, concludes that:

Bei solchen Reaktionen, welche den Gesamtorganismus beeinflussen, wird in den weitaus meisten Fällen die Bildung eines chemischen Körpers angenommen werden müssen, der in einer Anfangsreaktion entstehend nun an der betreffenden Stelle seine Wirksamkeit entfaltet. Alles, was nach der Bildung dieser photochemisch erzeugten Substanz geschieht, würde sich ebenso abwickeln, wenn ein solcher Stoff auf anderem Wege entstanden wäre. Anfänge, solche photochemisch entstandenen Körper zu identifizieren, sind in sehr bescheidenem Masse vorhanden. Es ist das Gebot der Stunde, solche Stoffe zu isolieren und dadurch die Wirksamkeit des Lichtes zu beweisen.

In these semicoenobes functional and tissue differentiation apparently have not proceeded so far as to involve the development of such centres of control. That myxamoebae influence each others movements and differentiations by chemical substances which they produce and set free seems, as I have pointed out, to be a natural assumption, especially for the period of their synallactic assembling. The chemical as well as the contact and pressure relations of the cells in the pseudoplasmodium at all stages of its formation and development into the sorocarp call for careful study. We have in *Polysphondylium* the appearance at least, of a cormophytic system which is influenced photomorphotically in its entirety (size and proportions). And the possibility is suggested that apparently systemic effects may be produced through intercellular reactions which are local, both in their initiation and their final expression. It would seem that *Polysphondylium* is an organism in which metameric differentiation, the formation of branches in whorls, the characteristic rate of taper in stipes and branches, may all be achieved locally by cellular interactions controlling cell movement and differentiation.

Etiolation. It was early recognized that the basic problem in etiolation is whether its common expression, in excess increase in length of the internodes and relatively small size of the leaves, involves, for the stems, increase in the number of cells by division (census growth) or increased mass growth and length of the individual cells, and for the leaves whether their relatively small size is due (1) to their having fewer cells or (2) smaller cells or (3) whether both differences exist in leaves of etiolated plants as compared with leaves on plants grown under normal conditions of illumination. It can hardly be claimed that the study of either of these problems has led

as yet to final and convincing results. MacDougal (1903) has summarized the data from the literature very adequately.

It is of interest to note that in the attempt to analyze the effect of light in checking growth and inducing bending, Vines (1886, p. 398) on the basis of his earlier work in Sachs' laboratory, develops the conception that:

The effect of the tonic action of light in diminishing the rate of growth is probably to be ascribed to an interference with the motility of the protoplasm of the growing cells. We may regard then, the tonic action of light, manifested in its retarding effect upon the rate of growth as an inhibitory action, and as being due to the induction of a certain degree of rigidity in the protoplasm, the rigidity being slight at low intensity and gradually increasing with the intensity until under the influence of very intense light, it is complete.

Again (p. 581) in discussing the curvature of unicellular organs Vines says:

Without pretending to say precisely what these changes may be, we may suggest that they consist in a modification of the motility of the protoplasm on one or both sides of the cell. The motility of the protoplasm of the concave side may be diminished or that of the convex side may be increased, or as is more probable, in view of the curvature of multicellular organs both of these effects may be simultaneously produced.

The possibility that these conceptions of Vines are in line with the evidence given by Lepeschkin (1931) and others that light increases the permeability of protoplasm is also to be considered.

Baranetzky (1875) reported that plasmodia tend to become immobile and ultimately abnormal in light, forming more thickened masses or strands as compared with the delicately reticulated appearance of normal plasmodia.

Brotherton and Bartlett (1918) studied the length of the epidermal cells of normal and etiolated epicotyls of *Phaseolus multiflorus* and conclude that the specific mean length of cells about to divide is the same in both light and darkness. However, as a result of excess increase in length of etiolated cells 34 per cent of the increase in length of the etiolated epicotyl is to be accounted for by increased cell division. It would seem that, since cell division only affects length where followed by cell elongation, this 34 per cent might best be called secondary etiolation resulting from a law of specific cell size. The basic factor in etiolation (66%) would then be, according to their argument, increased elongation of cells in darkness. They find that darkness favors, and light retards, elongation and has no direct effect on the rate of cell division. This is true of *Polysphondylium* if cell elongation and cell movement can be found to have a common basis. However, Brotherton and Bartlett find also that certain elongated meristem cells grown in darkness and not showing 'secondary divisions' may have a mean length of 0.149 mm., not well below but above the length of undivided cells (0.140 mm.) grown under ordinary conditions of illumination, which they explain as due to slenderness or some other cause.

Organization. When, as in the higher plants, the cell units remain in tissue continuity as they grow and divide it may seem possible to regard the whole cormophyte from its beginning in the egg as an integrated and differentiated mass of protoplasm. That this is not true of either the swarm of myxamoebae or the pseudoplasmodia and that the individual amoebae are in no sense specified as to their position in the finished sorocarp is obvious and can be illustrated experimentally by showing that out of a given swarm without further growth or cell divisions either one or several sorocarps of varying sizes and proportions may be made to develop. The process of aggregation and integration may be interrupted after it has been initiated and is well advanced and the number of ultimate unit systems may be changed.

It is obvious that we are here observing the actual process of achieving a higher unity by the free reactions and interactions of a swarm of units of a lower order whose individual unity and organization in no way resemble or directly represent the type of unity achieved in the sorocarp. The myxamoeba is a uninucleated mass of protoplasm creeping by pseudopodia and dividing more or less periodically. The sorocarp is an erect, radially and metamerically symmetrical structure simulating the cormophytic organization of the higher plants. The passing from one stage to the other is visible integration, the expression of the inherited and spontaneous activities of the amoebae limited and more or less directed by internal and external environmental stimuli.

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The genetics of Neurospora

I. The inheritance of response to heat-treatment

CARL C. LINDEGREN

(WITH FOUR TEXT FIGURES)

In the Ascomycetes, the eight ascospores, usually produced in a durable sac, are the result of meiosis of a single nucleus. Moreover, the sacs in some species are long and narrow. The products of division are not jumbled together, but are arranged in a row, so that their positions indicate their relationships. Micromanipulation and aseptic culture technique enable one to isolate these ascospores in order, and to study the genetic characters of the mycelia resulting from their germination. But the question of nuclear fusions and reductional divisions in the Ascomycetes has received many contradictory interpretations at the hands of different writers. The same form has been described as being parthenogenetic, or as having a single sexual fusion, or a double sexual fusion. Scarcely less divergent are the interpretations of the divisions in the ascus. There seems to be a general agreement that the chromosomes undergo what resembles a meiotic division, but the smallness of the chromosomes, and the difficulty of counting them, has led to a variety of interpretations.

An analytical knowledge of the genetics of an organism depends upon coördinating the nuclear history with the genetic behavior. This means that before the mechanism of meiosis can be studied by means of the arrangement of the ascospores in a long ascus, nuclear history and sex phenomena must be known accurately. Once they are understood, the Ascomycetes should provide excellent objects for studying the immediate effects of meiosis.

MICRODISSECTION AND CULTURE METHODS

Dodge (1928) and Wilcox (1928) began the genetic study of the ascomycetous genus *Neurospora* by isolating the spores of individual asci. They germinated each ascospore separately and cultured its mycelium alone. In order to continue this work, their methods have been refined. Microdissection by hand has been abandoned and a micromanipulator (text fig. 1), which is more readily adjustable than screw micromanipulators, has been devised. It is also much cheaper, being made chiefly of wood and containing no screws. Its base is a wooden block $50 \times 15 \times 5$ cm. In the midline of the block there is a groove 2 cm. deep, 2 cm. wide, and 10 cm. long. A steel rod 60 cm. long, 1 cm. in diameter, fits solidly in a hole bored vertically through the groove at the side which will be nearest the microscope. A brass tube, 1 cm. inside diameter, slides easily up and down this
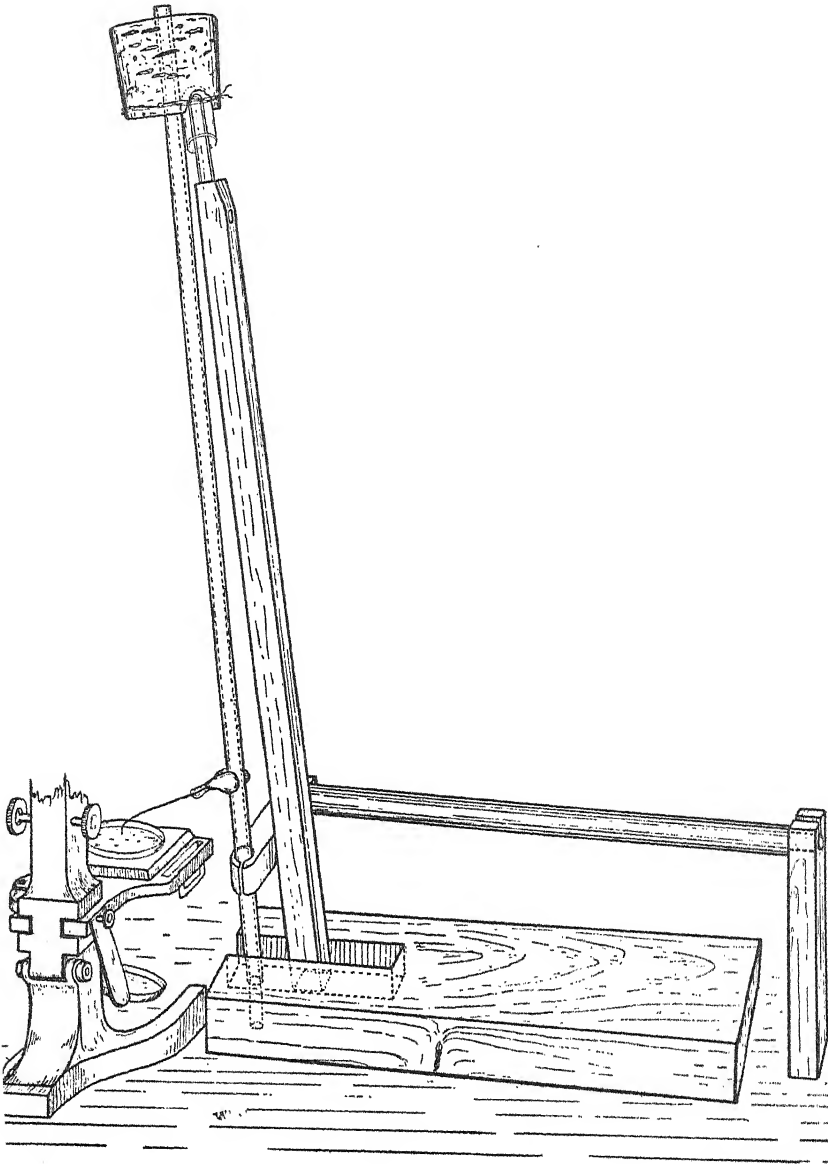
Fig. 1. Wooden micromanipulator ready for use. The needle is set by hand so that just clears the agar when the slanting rod is close to the brass tube. Then by moving : rod away from the tube with the right hand and pulling the plate away with the t hand, a single spore may be 'hoed' out of the ascus. This instrument with some provements can be obtained from Mr. L. L. Konrad, care of Spencer Lens Co., San incisco, California.

rod. Three-eighths inch curtain rod and three-eighths inch inside diameter
brass tubing, obtainable in any hardware store, are sufficiently accurate.
A needle, inserted in a short glass rod, is stuck to the brass tube with mod-
eling clay so that it just clears the surface of the microscope stage. Move-
ment of the needle in an arc about the vertical steel rod is obtained by a
wooden lever pointing away from the operator. The base of the brass tube
fits solidly in this wooden lever. The direction of motion of this lever is
changed by attaching at right angles a one-half centimeter wooden rod
placed so that its free end is conveniently situated at the right hand of the
operator. The free end of this rod is fitted solidly in an upright wooden
handle which rests upon the table. The wooden rod must have enough
spring so that it will allow the handle to rest on the table while the brass
rod is being moved upward and downward. Sensitivity of the movement
in the arc about the steel rod depends upon the length of the needles rela-
tive to the length of the wooden lever, by the principle of similar triangles.
For moderate magnifications one to five sensitivity is sufficient, using a
10 cm. needle and a 50 cm. lever.

Movement of the needle point in a vertical direction is obtained by the
following device: A large cork is firmly fitted on the upper end of the brass
tube. A 2 cm. test tube, which has been cut off about 2 cm. from the base,
is fitted solidly in a hole in the base of the cork. A wooden bar $50 \times 2 \times 2$
cm. stands obliquely, and its lower end slides in the grooved base. Its upper
end is tapered and rounded to articulate in the cup formed by the base of
the test tube. Up and down movement of the needle is obtained by sliding
the lower end of this bar along the groove, toward or away from the verti-
cal rod. To determine the sensitivity of this movement, let the length of
the oblique bar which forms the constant hypotenuse of a variable right
triangle be equal to a. Let the horizontal side (groove) equal x and the
vertical side (brass tube and a steel rod) equal y.

$$Then \ x^2 + y^2 = a^2$$

By implicit differentiation with respect to x

$$\frac{dy}{dx} = \frac{-x}{y}$$

The sensitivity thus depends inversely upon the ratio of the variable
horizontal side to the variable vertical side of the triangle. Therefore, the
horizontal side must be short to give maximum sensitivity. It is possible
to work with a horizontal side of about 1 cm. with the vertical side of
about 50 cm., thus minimizing the manual movement about fifty times.

Chromel needles were used. They were made by hammering a piece of
wire very thin and cutting to a fine point with scissors. After the last cut

the wire was again hammered to produce a hoe-like end rather than a pointed one.

The dissections were performed on clear three per cent agar, as follows: Perithecia were crushed between flamed microscope slides and a drop of water was added from a sterile lip pipette. The asci emerge from the perithecia in groups and the clusters can be easily picked up with the pipette and placed on the agar. These asci, still attached to the ascogenous hyphae, spread out radially on the agar. Then individual asci are dissected off as soon as the drop has dried out. The location of the spores in an ascus is indicated by numbering from one to eight; the spore at the outer end of the ascus being number one. The thin but broad hoe-like end of the needle is dropped between the first and second spore and the plate pulled away by hand, thus breaking the ascus wall. A mechanical stage is not necessary to hold and move the plate, although some workers might desire it. All eight spores are dissected—'hoed' out—one by one, and placed in a row. Then they are transferred individually to a second plate set up under a second binocular, so that there is no difficulty in returning to the row of ascospores in the first plate. The position which a spore occupied in the ascus is indicated by a number marked in the agar beside it.

Heat-treatment is used to germinate the spores. They are then transferred individually to agar in small tubes (9 by 100 mm. or 3/8 by 4 inches) by cutting out the small piece of agar containing each germinated spore under a binocular microscope. The heat-treatment kills any conidia which might have been transferred with the ascospores into the agar plate. The transfer of the germinated spores to small tubes is made in a $3 \times 3 \times 6$ foot glass chamber which has been liberally sprayed with dilute alcohol and wiped down with mercuric bichloride solution.

The small tubes are kept in racks made of pressed cork strips. This pressed cork is 3 mm. thick and is cut in strips 2×30 cm. About sixteen holes, each 9 mm. in diameter, are punched in the strips with a cork borer. The culture tubes are inserted in the same order in which they occur in the ascus and are held tightly enough in place so that they cannot fall out. These strips of tubes are mounted in wooden racks.

HEAT-TREATMENT METHODS

Dodge (1912) has shown that the ascospores of certain species of the Ascobolaceae, which do not ordinarily germinate in the laboratory, can be induced to germinate by heating. The spores are placed on agar in Petri plates, and the plates are put in a gas oven, which is then regulated, so that the temperature rises to about 70° C. in about twenty to thirty minutes. The plates are then removed. In some species, some spores fail to

germinate even after this treatment. Dodge has since shown, in other papers, that this method may be employed successfully in inducing ascospores of certain species of *Aleuria, Lachnea,* and *Neurospora* to germinate. This method has also been employed by Ramlow (1915), Betts (1926), Wilcox (1928), and others. The writer has conducted a series of experiments on ascospore germination and describes below a more refined, but not necessarily infallible, method of heat-treating spores of *Neurospora.*

Experiments to determine an optimum heat-treatment

In studying heat-treatment, spores of *Neurospora tetrasperma* were placed on agar in small Petri dishes. The depth of the agar varied from three to seven millimeters. The dishes were placed on a one-eighth inch thick copper plate, set on top of a Columbia paraffin oven. The copper was allowed to come to a stable temperature (73–77° C.) before the Petri dishes were placed on it. A few drops of water under each dish insured a good contact. The temperature at the surface of the agar gradually rose from the original room temperature of about 20° C. to nearly 70° C. Temperatures were determined by the melting points of various organic compounds. These were placed on thin cover glasses, a series of which were laid on agar in Petri plates containing no spores. After many trials, the compounds shown in table 1 were selected. The compounds began to melt

TABLE 1

Compounds used as thermometers

| COMPOUND | MELTING POINT | TIME OF MELTING IN MINUTES | |
		Plate 1	*Plate 2*
Benzophenone	47.5°–48.5°C.	6.5– 9.0	8.0– 11.0
Betabromnaphthalene	53.0°–55.0°C.	32.0– 34.0	38.0– 42.5
Betachlornaphthalene	56.5°–57.0°C.	39.0– 40.0	49.0– 51.0
Palmitic acid	61.0°–61.5°C.	61.0–100.	75 –105
Stearic acid	69.0°–69.5°C.	240	240

at the lower temperature given and were completely melted at the higher temperature. The table also shows the times at which the compounds melted in two blank plates, of different thickness of agar. Thus the approximate temperatures of the ascospores on the surface of the agar on another plate, heated simultaneously with the 'thermometer' plate, were determined. The main errors of this method are: (1) raising the cover of the 'thermometer' plate to wipe off the moisture film, for observation of melting points, obviously cools this plate below the temperature of the spore-bearing plate; (2) the lowering of the melting point of the organic compounds due to mixture through distillation; (3) the irregular heating

of different plates due to differences in size, agar depth, position, contact, etc. It is questionable if a better method for determining the temperature would be worth the trouble, because the variation among the several plates is probably considerable. A series of experiments was performed to determine the optimum time of heat-treatment. Sixty-seven Petri dishes containing spores of *N. tetrasperma* were treated for different lengths of time on the copper plate. Blanks were used with the organic compounds as thermometers. The results corresponded roughly with those shown in table 1. After sufficient time was allowed for germination of all spores capable of germination, counts were made. Each percentage recorded is the final count from a single plate containing from forty to several hundred spores, generally more than a hundred. Table 2 shows the data, and text figure 2 is a graph showing the relation between the duration of heat-treatment by the copper plate method and the percentage of germination. These are the total data from sixty-seven Petri dishes, each containing on the average well over a hundred ascospores.

TABLE 2

Germination counts on sixty-seven Petri dishes containing Neurospora tetrasperma ascospores heat-treated by the copper plate method for various lengths of time

TIME MIN.	PER CENT	TIME MIN.	PER CENT	TIME MIN.	PER CENT	TIME MIN.	PER CENT
11	2	25	100	46	98	90	95
12	0	26	92	48	99	100	97
13	0	26	97	50	97	110	92
14	7	27	100	52	85	120	93
15	1	28	96	54	93	130	82
16	3	29	95	54	98	140	94
17	0	30	98	56	56	150	78
18	2	30	100	58	78	160	0
18	4	31	97	59	94	170	35
19	2	32	98	62	88	180	11
19	30	33	93	66	81	190	8
20	81	34	98	68	92	200	0
21	88	34	95	70	97	210	1
22	63	38	99	74	93	220	1
23	77	40	98	78	97	230	2
24	84	42	80	82	93	240	3
25	86	44	98	86	97		

In analyzing text figure 2, it can be seen that the optimum heat-treatment has a rather long range, namely, from twenty-five to forty minutes. It may be concluded that a heat-treatment of from twenty-five to forty minutes, with the temperature rising from approximately 54° to 58° C., will give very high percentages of germination. There is evidence to show

that lower temperatures for longer times will give the same results, but no effort has been made to determine a critical temperature.
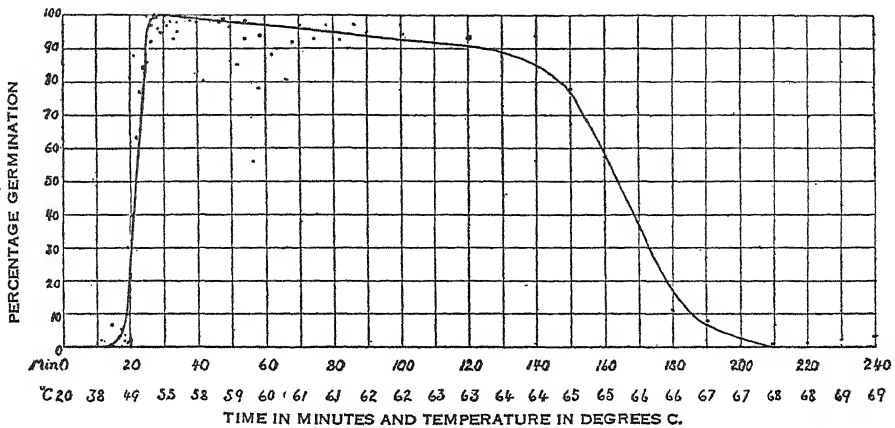

Fig. 2. Graph showing the percentages of germination obtained in 67 different agar plates placed on the copper plate for various lengths of time. The temperature of the agar during the time the dish was on the copper plate is also shown. Note the flat maximum and the rapid increase beginning at about 20 minutes, as well as the rapid fall after 140 minutes.

Experiments on killing conidia

The peculiar advantage of using *Neurospora* for genetic studies lies in the fact that the conidia and mycelia, which may be accidently transferred with the ascospore, are killed by the heat-treatment which induces the ascospore to germinate. After the ascospores have germinated, fifteen to eighteen minute heat-treatments by the copper plate method are sufficient to kill the mycelium of the germinated spores.

In these experiments an eighteen minute treatment raised the temperature of the growing mycelium from room temperature to about 48° C. Later a thermostat-controlled chamber was used instead of the copper plate for heat-treating the spores. The temperature was constant at 58° C., and the plates were treated for sixty minutes. To test whether this treatment was sufficient to destroy the conidia, young conidia of *Neurospora tetrasperma* were treated. The untreated conidia showed 100 per cent germination on cornmeal agar. Ten minutes in the thermostat at 58° C. delayed germination for as long as two days, but practically all of the conidia eventually germinated. From 45 to 70 minutes heating at 58° C. killed all the conidia in thirteen of the small plates used, and no later growth was produced, although they were held for ten days. In two cases out of fifteen, however, (one Petri plate held for sixty minutes and the other for sixty-

five minutes) the plates were overgrown when examined five days later. It is probable that only a small number of conidia survived in these plates. In general the asci are carefully washed and no conidia are carried over. The chances of any conidium, which might accidently be carried over, surviving the sixty minute treatment are evidently not great.

Random single ascospore cultures of *N. crassa* were often made by using conidia and ascospores on an agar plate and allowing the conidia to germinate. Then the plate was heat-treated and the ascospores transplanted to tubes. As a control many of the germinated, and subsequently heat-treated, conidia were also transplanted, but none ever grew.

INHERITANCE OF 'RESPONSE TO HEAT-TREATMENT'

In the present method of heat-treating ascospores, the copper plate is no longer used. It was thought that longer treatments, at lower temperatures, gave greater reliability with less injury, and hence fewer killed spores. A small thermostat was built for this low temperature treatment. In the early part of the work, it was thought that cooling the Petri plates containing the spores down to about 10° C., for 12 to 24 hours before heating, increased the certainty of germination. Recent experiments show that cooling has no such beneficial effect.

It was determined that the optimum heat-treatment for a cooled Petri plate in the thermostat held at 58°C. was one hour. The thermostat is so small that its temperature drops to about 45°C. on introducing the cooled plates, and does not attain 58°C. until about 20 minutes later. It may be that the ascospores on the surface of the agar never quite reach the temperature which the thermometer in the thermostat indicates.

In the course of the work the spores from over 500 individual asci were isolated in order, one by one, so that their positions in the particular asci were known. Only asci containing eight ripe spores were used. These spores were incubated on agar over night at room temperature to determine if any germinated without heating, and if any conidia had been carried over with them. At first all plates were cooled as above noted before heat-treating, but later the cooling was abandoned. The plates were then treated in the thermostat held at 58°C. for one hour. About ten hours later the germinated spores were removed to culture tubes, and those which had not germinated were treated for a second and sometimes for a third hour. Table 3 gives a record of the asci (from the 500 asci of *N. crassa*) in which ascospores were found that germinated without heating or that responded to heat-treatment of longer than one hour. Less than one per cent of the total number of spores germinated without heat-treatment; about four-fifths of the total number germinated following the first hour of treatment,

about two per cent of the spores yielded to the subsequent heat-treatments, and about one-fifth of the spores failed to germinate. The ratio in which the different types of spores occurred in certain asci, and their distribution in the ascus, suggest genetic differences, but these supposed differences have not been adequately tested.

TABLE 3

Fifty-two exceptional asci of Neurospora crassa from a total of over 500 studied. These are exceptional in containing some ascospores which did not respond to heat-treatment in the ordinary manner.

ASCOSPORE	1	2	3	4	5	6	7	8	ASCOSPORE	1	2	3	4	5	6	7	8
Ascus									*Ascus*								
217	1	1	1	1	2	2	x	2	642	1	2	x	1	3	3	2	1
222	1	x	1	1	1	2	1	1	643	1	1	1	1	1	2	1	1
257	1	1	1	1	1	1	2	1	644	2	2	2	2	x	x	2	2
286	1	0	0	1	x	1	1	1	646	2	x	1	1	1	1	2	1
312	1	1	x	2	x	x	x	1	650	1	2	1	2	1	x	1	1
322	x	2	1	1	x	1	1	1	651	2	2	2	2	1	1	1	2
330	1	1	1	1	0	0	0	0	654	2	1	1	1	1	1	1	1
332	1	2	x	2	2	2	x	2	655	1	2	2	2	1	1	1	1
336	2	1	2	2	1	1	x	2	657	1	1	1	1	1	1	1	2
340	x	1	1	2	1	1	1	2	659	1	1	1	1	2	1	1	1
341	3	2	1	2	1	1	1	1	676	1	1	1	1	1	1	2	1
342	ab	ab	ab	ab	1	2	2	2	677	1	2	1	1	1	2	1	1
361	1	1	x	1	0	0	x	x	678	1	2	1	1	1	1	1	2
498	x	1	1	1	0	x	0	1	683	x	1	2	1	1	1	1	1
500	1	1	1	1	1	1	0	1	688	1	2	1	1	1	1	1	1
550	1	1	2	2	2	1	1	1	715	2	2	1	x	1	1	1	1
551	2	2	x	x	1	1	1	1	718	1	2	1	1	1	1	1	1
552	1	2	2	2	2	2	1	1	724	1	1	1	1	1	2	1	2
553	1	1	1	1	2	2	2	2	725	1	1	1	1	1	1	2	1
554	1	1	1	1	2	2	2	2	730	1	1	1	1	1	1	1	2
555	1	1	2	2	1	1	1	1	731	1	1	1	1	1	2	2	1
556	1	1	2	2	2	2	2	1	732	1	1	1	2	1	1	1	1
557	1	1	2	1	1	1	1	1	741	2	3	2	2	3	1	2	2
562	1	2	1	x	1	1	1	1	744	1	2	2	2	3	1	1	1
563	2	x	1	0	x	0	2	2	745	2	3	3	x	x	x	2	2
641	2	2	3	3	1	x	3	3	690	1	1	1	1	2	2	2	2

Legend

1—spore germinated after first hour heat-treatment
2—spore germinated after second hour heat-treatment
3—spore germinated after third hour heat-treatment
0—spore germinated without heat-treatment
x—spore did not germinate
ab—spore aborted

In order to test this point selection experiments and subsequent crosses would have to be made. Only one experiment was performed. A mating was made between the mycelia from two of the ascospores that germinated without heating. Fifty-nine ripe ascospores were selected from the off-

spring. They were incubated on agar at 27°C. for nearly two days, but none germinated. A one hour heat-treatment induced fifty-five of them to germinate, indicating that they were mature. At first this was supposed to indicate that variations from response to one hour heat-treatment were not inherited. But subsequent experiments, with crosses of definitely in herited types, gave similar first generation results. Further generations, which in this case were not raised, would be required to prove this point.

It must also be noted that these asci were the inbred descendents from an ascus in which the spores germinated following a treatment of one hour, and it is possible that other races of *N. crassa* may exist whose spores require heat treatment for different lengths of time.

Nine asci of *N. sitophila*, described in table 4, showed a striking contrast to the case of *N. crassa*. It must be noted that all the asci of *N. sito-*

TABLE 4

Nine asci of Neurospora sitophila showing the positions of the asocspores and the manner in which they responded to heat-treatment

ASCOSPORE	1	2	3	4	5	6	7	8	ASCOSPORE	1	2	3	4	5	6	7	8
Ascus									*Ascus*								
202	x	x	2	2	2	2	x	x	206	2	2	2	2	1	1	1	1
203	2	2	2	2	2	2	2	2	207	1	1	1	1	2	2	2	2
204	1	1	1	1	1	1	1	1	208	3	x	3	x	2	2	x	x
205	1	1	1	1	1	1	1	1	209	1	2	2	2	2	2	2	x
									210	1	2	1	2	1	2	1	1

Legend
1—spore germinated after first hour heat-treatment
2—spore germinated after second hour heat-treatment
3—spore germinated after third hour heat-treatment
x—spore did not germinate

phila studied appear in table 4, while table 3 includes fifty-two aberrant asci selected from a total number of over 500. Therefore, in the case of *N. sitophila* about one half of the spores required two hours heat-treatment, while less than half of them germinated after one hour treatment.

In the case of asci 202, 206, and 207, the arrangement of the spores might suggest a segregation of a factor determining the response to heat-treatment, but no further breeding tests were made.

That the type of treatment necessary for germination depends on genetic factors is indicated clearly by the following experiments, which were started for another purpose, namely, to test the nature of a supposedly hybrid strain produced by Dodge (1931). By crossing a non-conidial mutant of *N. sitophila* with typical conidial *N. tetrasperma* and selecting and back crossing for several generations he had first secured a non-conidial

4-spored race. Then from this non-conidial, 4-spored type he grew a bisex-
ual, hermaphroditic, non-conidial mycelium, which he designated 3C. He
mated this with a unisexual, conidial mycelium of *N. tetrasperma*, pro-
ducing thereby perithecia which were supposedly hybrid.

Proof that a hybrid had been produced between the hermaphroditic
and the unisexual mycelium would be furnished if both conidial and non-
conidial ascospores were found in the same ascus. The writer accordingly
dissected sixteen exceptional 5-spored asci from this 4-spored hybrid.
Since one parent was non-conidial and the other was conidial, 5-spored
asci were selected in the expectation that, if a cross had been made, one of
the two small unisexual spores from each of these asci would show the
character of one parent while the other would show the character of the
second parent. In each of the three other standard, bisexual, hermaphrodit-
ic spores, containing two genetically different nuclei, one from each par-
ent, masking of the non-conidial character might be expected. As table 5
shows, all mycelia from the bisexual ascospores did produce conidia, indi-
cating that the non-conidial character, if present, was masked. That the
non-conidial character was actually present was shown by its manifesta-
tion in about half of the mycelia from the small spores. The presence of
the conidial and the non-conidial nuclei proves that the supposed hybrid
had actually been produced by the cross.

The data in table 5 are represented diagramatically in text figure 3.
The 5-spored asci are grouped in classes according to the arrangement of
the two small spores and the types of mycelia produced. The nuclei are
shown as white, black, and black with a white center. The white nuclei
indicate sex A; the black, sex B; the black nuclei with white centers were
probably sex B but were incompatible with the tester strains used, so can-
not be definitely determined in every case. Incompatibility is sterility with
tester strains of opposite sex, a phenomenon resembing self sterility. The
large, i.e., standard-sized, spores were assumed to be binucleate in origin,
and the small spores uninucleate. Table 5 shows that the nuclei in most of
the large spores contained two compatible nuclei, their sexes being indi-
cated by $A+B$. A few of them carried incompatible nuclei, for the mycelia
failed to produce perithecia. In such cases the sex is indicated by $A+B$?.
The sign $+C$ indicates that the mycelium from the spore produced conidia,
while $-C$ indicates that it was non-conidial. The mycelia from all of the
large spores (except from two in ascus 408, discussed in detail below) pro-
duced conidia. Of the two small spores in each ascus one was conidial and
the other was non-conidial (with the exception again of ascus 408, where
both were $+C$). It is obvious from text figure 3 that the perithecia were
true hybrids, since half of the nuclei in each ascus contained the conidial

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TABLE 5

Ascospores dissected from fourteen asci obtained from hybrid perithecia referred to in the text. It is indicated whether or not the mycelia produced conidia, and whether or not the spores needed heat-treatment to induce germination.

SPORE	1	2	3	4	5
Ascus 402	L H +C A+B	L W +C A+B	S H +C B?	L H +C A+B?	S W −C A
Ascus 406	L H +C A+B	L H +C A+B	S H +C B?	L H +C A+B	S W −C A
Ascus 411	L H +C A+B	L H +C A+B	S H +C B?	L H +C A+B	S W −C A
Ascus 412	L W +C A+B	L H +C A+B	S H +C B?	L W +C A+B	S W −C A
Ascus 413	L H +C A+B	L NG	S H +C B?	L H +C A+B	S W −C A
Ascus 404	L H +C A+B	L H +C A+B	S H +C B	L H +C A+B	S W −C A
Ascus 410	L H +C A+B	L H +C A+B	S H +C B	L H +C A+B	S W −C A
Ascus 405	L W +C A+B	L W +C A+B	S W −C B?	L H +C A+B	S H +C A
Ascus 407	L H +C A+B	L H +C A+B	S W −C B?	L H +C A+B	S H +C A
Ascus 415	L H +C A+B	L H +C A+B	S W −C A	L H +C A+B	S H +C B?
Ascus 417	L H +C A+B	L H +C A+B	S W −C A	L H +C A+B?	S H +C B?
Ascus 403	L H +C A+B	L H +C A+B	L H +C A+B?	S W −C A	S H +C B?
Ascus 416	S W −C A	L H +C A+B	S H +C B	L H +C A+B	L H +C A+B
Ascus 408	L W −C A	L W −C A	S H +C B	L H +C B	S H +C B

Legend. L—Large, or standard sized, binucleate spore; *S*—Small spore, uninucleate; *H*—Spore needed heat-treatment to induce germination; *W*—spore germinated without heating; +*C*—Mycelium produced conidia; −*C*—Mycelium failed to produce conidia; *A* and *B*—Sex A or B; *A+B*—hermaphroditic, bisexual; *B*?—Sex B, incompatible with tester used; *A+B*?—hermaphroditic but producing no perithecia; *NG*—not germinated.

factor and half the non-conidial factor. Moreover, when a non-conidial and a conidial nucleus were present in the same ascospore, the mycelium produced conidia.
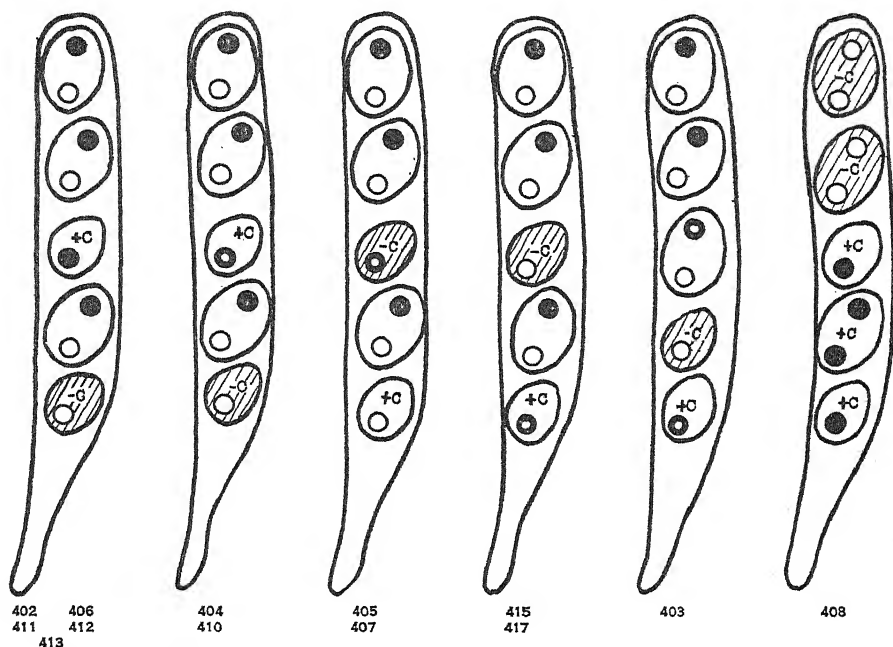
Fig. 3. Diagram of thirteen 5-spored asci dissected from a hybrid obtained by Dodge. The size, arrangement in the ascus, sex, and incompatibility of the spores are shown. The presence or absence of conidia on the mycelium and whether or not the spores require heat-treatment to induce germination are also shown. White nuclei are sex A; black nuclei are sex B; black nuclei with white centers are sex B incompatible; cross-lined spores germinate without heat-treatment; open spores require one hour heat-treatment; $-C$, the mycelium develops no conidia; $+C$, the mycelium develops normal conidia.

The special interest of this hybrid lay in the fact that Dodge had found that a large proportion of the spores germinated without heat-treatment. This characteristic appeared clear-cut in the spores dissected from the asci just described. In text figure 3, the diagonally lined spores are those which germinated without heating. The figure shows also that the spores which germinated without heating were all non-conidial. In all but two asci (405 and 407) these non-conidial spores that germinated without heating were moreover of sex A. This three-character linkage was very striking.

Ascus 408 was exceptional in two respects; first, the small spores were alike $(B, +C, H)$, second, the three large spores were unisexual instead of hermaphroditic, and two were $-C$. This anomalous situation can be ac-

counted for in terms of the known peculiarities of the spindles leading to the formation of the spores, provided the segregation for these characters occurs at the second division. Dodge (1927) has described in detail the arrangement of the spindles in *N. tetrasperma*, showing that first-division segregation of factors for sex would always produce four hermaphroditic spores in each ascus. Since Dodge found no binucleate unisexual spores, he was of the opinion that segregation of sex factors always occurred at the first division, or that if segregation occurred at the second division, the orientation of the nuclei was such that unlike sexes came together. Without this peculiar orientation, second-division segregation would produce binucleate unisexual spores. Ascus 408 is of particular interest, since all three of the binucleate spores were unisexual, and hence presumably lacked this special orientation of the nuclei. Assuming that this hybrid has the same spindle mechanism as *N. tetrasperma*, we may conclude that ascus 408 shows second-division segregation of the sex factors as well as those for conidia and those for germinating without heating. Text figure 4 is a diagram showing the type of ascus behavior necessary to produce this rare kind of ascus. The straight lines are the axes of the spindles as they would
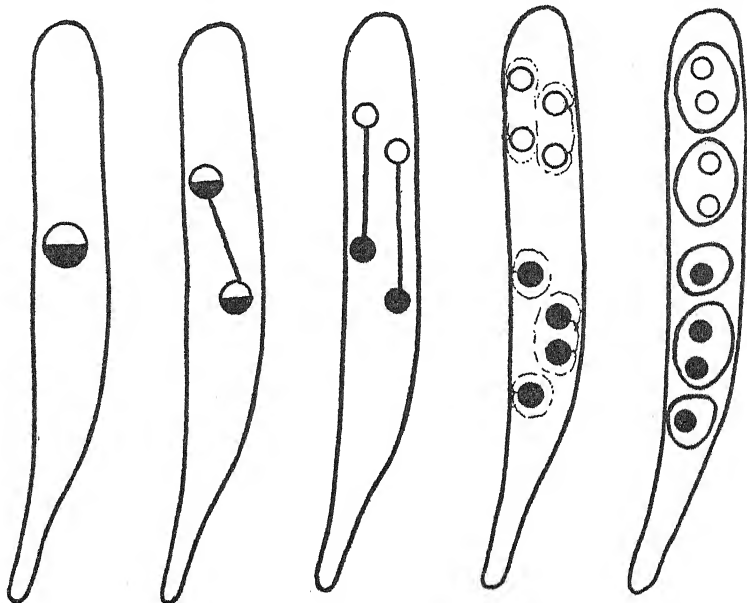
Fig. 4. Diagram showing how second-division segregation of the factors determining sex, response to heat-treatment and the presence or absence of conidia could give rise to a 5-spored ascus such as ascus 408, containing no hermaphroditic spores. White nuclei contain the factors for sex *A*, absence of conidia and ability to germinate without heat treatment. Black nuclei contain the factors determining sex *B*, production of conidia and inability to germinate without heat treatment.

lie if they followed the arrangements found for *N. tetrasperma*. This differs from Dodge's diagram for second-division segregation in only one feature, namely, that the orientation of one of the nuclei is reversed in the binucleate state of the ascus (text fig. 4).

The failure to produce perithecia in the case of the mycelia from spores from ascus 408 cannot be ascribed to incompatibility, since it was only sex *B* that showed incompatibility in this hybrid and in ascus 408 the sex *B* strain was tested and found compatible with the tester strain. That the failure to produce perithecia was actually incompatibility in the case of some of the mycelia of other asci was shown by the fact that the sex *B* strain from ascus 407, which failed to fruit with tester strains, fruited readily when mated with the sex *A* strain from ascus 406. This cross (406–5×407–3) was the mating of two mycelia both of which were non-conidial and were produced by ascospores which germinated without heating.

Twenty-one 4-, 5-, and 6-spored asci, from the cross 406–5 by 407–3, were dissected and the spores incubated at room temperature for several days. Table 6 shows the ascospores from this group which germinated

TABLE 6

Twenty-one asci dissected from a cross of two non-conidial ascospores that germinated without heating. The size and arrangement of the spores in the ascus are shown and whether or not they germinated without heating. Abbreviations as in table 5.

ASCOSPORES	1		2		3		4		5		6	
Ascus 1	L	H	L	H	S	H	L	W	S	W		
Ascus 3	S	H	S	W	L	H	L	H	L	H		
Ascus 4	L	W	S	W	S	H	L	H	L	W		
Ascus 5	L	W	L	W	S	H	L	H	S	W		
Ascus 6	S	W	L	W	S	H	L	H	L	H		
Ascus 7	L	W	L	H	S	W	L	H	S	H		
Ascus 9	L	H	L	W	S	W	L	H	S	H		
Ascus 10	L	H	L	H	S	H	L	H	S	W		
Ascus 14	L	H	L	H	S	W	L	W	S	H		
Ascus 15	L	H	L	H	S	W	L	H	S	H		
Ascus 17	S	H	S	W	L	H	L	W	L	H		
Ascus 18	L	W	L	W	S	H	L	W	S	W		
Ascus 20	S	W	L	H	L	H	L	H	S	W		
Ascus 16	S	H	S	H	S	W	S	W	L	H	L	W
Ascus 2	L	W	L	W	L	W	L	W				
Ascus 8	L	W	L	H	L	H	L	H				
Ascus 11	L	H	L	W	L	H	L	H				
Ascus 12	L	H	L	W	L	W	L	W				
Ascus 13	L	H	L	W	L	W	L	H				
Ascus 19	L	W	L	W	L	W	L	W				
Ascus 21	L	W	L	H	L	W	S	W				

without heat-treatment. Forty-five per cent of the large spores germinated without heating. Only twenty per cent of the ascospores in the parent hybrid germinated without heating. It is remarkable that in only one case did both small spores germinate without heating.

We may conclude from these experiments that the factor causing ascospores to germinate without heating is hereditary, and that it is usually carried by nuclei of sex A.

SUMMARY AND DISCUSSION

A microdissection apparatus was devised to rapidly remove single spores in order from the ascus in a genetic study of *Neurospora.*

Experiments were performed which show that it is possible to determine the optimum heat-treatment which will cause the largest percentage of the ascospores of *Neurospora* to germinate. Furthermore, it was shown that the heat-treatment commonly used killed the asexual spores, thus simplifying the separation of sexual from asexual offspring.

The ascospores from the race of *N. tetrasperma* seemed to be highly uniform in their response to heat-treatment. There was evidence that part of the small percentage of variation after one hour heat-treatment in *N. crassa* was due to genetic factors. Dodge's hybrid and the race of *N. sitophila* produced two types of ascospores in regard to their response to heat-treatment. In both races the differences were the result of genetic constitution, but there was evidence that the ability of a spore to respond to heat-treatment depended to some extent on the environment. This was best shown by the fact that although all of the large spores in the hybrid had one nucleus containing a factor for germinating without heat-treatment, and one containing a factor determining response to one hour heat-treatment, some germinated without heating while others did not. In Dodge's hybrid, the unisexual ascospores fell into two genetic groups: in one group all of the ascospores germinated without heat-treatment; in the other group the ascospores required one hour heat-treatment to initiate germination. The race of *N. sitophila* contained two genetic groups as well. One kind of ascospore required one hour heat-treatment, and the other required two.

Despite the evidence that response to heat-treatment is a genetic character in these cases, it is improbable that it can be used extensively in a study of the genetics of *Neurospora*, because of its variability. In a closely inbred race, such as the race of *N. crassa*, which seemed to be rather uniform in its response to a one-hour heat-treatment, ascospores were encountered which germinated without heating and others which required a three-hour treatment. Although in a few cases, the order of the spores in

the ascus indicated that factors determining response to heat-treatment had been segregated, it was obvious in most cases that the pairs of ascospores resulting from the third division in the ascus sometimes responded differently. It will be shown in later papers that this division is invariably equational. This means that these pairs of ascospores are identical genetically. The fact that they sometimes responded differently indicates that environmental factors were also effecting the variation.

Faull (1930) concluded, on the basis of some experiments on heat-treatment of the ascospores of a strain of *N. crassa*, that heat-treatment does not increase the percentage of germination. The data which she presents do not justify this conclusion. She found that from 4 to 25 per cent of the ascospores in various random samples germinated without heat-treatment. Ascospores in various random samples which she heat-treated at 51.5°C. for one to four hours showed 5 to 94 per cent germination. Obviously she was working with a mixed strain producing at least two genetically different kinds of ascospores.

The interest of Dr. T. H. Morgan in this problem has been a great encouragement. During the summer of 1930, the writer enjoyed the facilities of the New York Botanical Garden through the generosity of the director, Dr. E. D. Merrill. While there, he was closely associated with Dr. B. O. Dodge, and, through this association, received many valuable suggestions which have greatly facilitated the pursuit of the work. Dr. A. H. Sturtevant and Dr. Albert Tyler have offered many valuable suggestions. The writer is grateful to Dr. Morgan, Dr. Dodge, and Dr. Calvin B. Bridges for their assistance in revising the manuscript.

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1927-1931

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Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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Control of gametophytic selection in Datura through shortening and splicing of styles[1]

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(WITH THREE TEXT FIGURES)

In the course of our experiments on the control of gametophytic selection, we found that restricted pollinations together with a division of the seed capsules resulted in a very marked increase in the pollen transmission of extra chromosomes in *Datura*.[4] This increase has, for the lower part of the seed capsule, ranged from 49 to 65 per cent with pollen from the 25-chromosome plant Cocklebur. By excision of the part of the style containing the slow-growing pollen tubes in similar pollinations, we obtained a complete non-transmission of the extra Ck. chromosome. In the experiments concerned in this paper, we shall describe a method by which a part of the style containing the more rapidly-growing pollen tubes may be excised and discarded. It follows that this manipulation should result in a nearly perfect pollen transmission of the extra chromosome, permitting the use of more pollen or making unnecessary the division of seed capsules. This procedure necessitated the development of a special technique for reuniting the two parts of the style which had been severed and shortened, or the joining of two different styles in a particular place.

Recently, the discovery of many genes obtained from irradiation whose effect on pollen-tube growth renders them non-transmissible, or only slightly transmissible through the pollen,[5] has stimulated renewed efforts in seeking methods for the control of gametophytic selection. These methods, therefore, fill a definite need in furthering the study of the lethals of pollen-tube growth. Aside from the splicing of styles, there are other manipulations which may ultimately prove successful where a mere shortening of the style is desired, as in the case of self- and cross-sterility.

Some interesting facts concerning pollen-tube behavior were discovered in the course of these investigations which may be advantageously described here. It happens that our technique for the study of the position

[4] Buchholz, J. T. and A. F. Blakeslee. Pollen-tube growth and control of gametophytic selection in Cocklebur, a 25-chromosome *Datura*. Bot. Gaz. 90: 366–383. 1930.

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of the pollen tubes and their distribution within the style at any desired time after pollination[6] has enabled us to observe many phenomena of pollen tube behavior, as well as to determine the success or failure of any type or condition of pollination. Without this technique, it would be difficult or impossible for us to know the degree of success attained in attempted crosses or the cause of failure in the various types of pollinations.

MUTILATIONS OF THE STYLE

We have made attempts to shorten the style by cutting off a portion and pollinating a small area of conducting tissue thus exposed on the wounded surface. In these trials, we found that, due to dessication, the pollen usually would not germinate; when protected against dessication about 20 pollen grains, at best, could be induced to germinate under the most favorable conditions. The exposed area of the conducting tissue was evidently too small. Cutting in diagonal increases this area slightly, but this gives a pointed, more exposed end.

By splitting the style through to the mid-point, placing pollen grains in this wound in direct contact with the conducting tissue, and holding these sides together by means of a straw cut from a grass culm, the pollen was found to germinate very satisfactorily. However, an examination showed that the pollen tubes were growing in both directions. Many of the pollen tubes (sometimes more than half of them) were directed toward the stigma end, where they stopped very close to the exposed style ends from which the stigma had been removed in attaching the straw. Others were growing in the normal direction toward the ovary. This peculiar behavior is of considerable interest in relation to chemotropism and pollen-tube growth. Regardless of this reversal in the direction of some of the pollen tubes, we became convinced from an examination of the dissected preparations, that, as a method of shortening the style, the pollination of the interior of a split style with suitable protection against dessication might be successful in practice, where a shortened pistil is desirable. East and Park[7] reported that they obtained two seed capsules in incompatible tobacco plants by the pollination of pistils which had been mutilated.

The reversal of pollen tubes calls to mind another observation first made nearly ten years ago. At that time, flowers were pollinated, kept in a cool, moist place for several days, and then re-pollinated with the idea of observing the amount of change in the growth-rate of pollen tubes in the

[6] Buchholz, J. T. The dissection, staining and mounting of styles in the study of pollen-tube distribution. Stain Technology. 6: 13–24. 1931.

[7] East, E. M. and J. B. Park. Studies in Self sterility II. Pollen-tube growth. Genetics. 3: 353–366. 1918.

partially depleted style of an old flower. A very pronounced decrease in the rate of growth was obtained in the pollen tubes from the second pollination, but a much more interesting phenomenon was observed, namely; that some of the pollen tubes from the first pollination were found to be growing in the reversed direction. They appeared to be emerging from the ovary and growing toward the stigma. An examination of the styles of 30 or more flowers two- and three-days after pollination (self and open pollinated flowers in the field) showed that in more than half of these preparations anywhere from 1–11 pollen tubes were growing in the direction of the stigma. In flowers only a day old, there were very few reversed pollen tubes.

Possibly we should revise some of the commonly accepted ideas concerning chemotropism and pollen-tube growth in the light of these observations. There is certainly a question as to whether chemotropism, if present, exerts its influence through the length of the style. If a pollen tube happens to become reversed in its orientation at any time, it will continue its growth toward the stigma. On the stigma there is only one direction in which a pollen tube may grow and find nutriment when the pollen grain germinates. All cells of the stigma and conducting tissue are so oriented that the path of least resistance (the long axis of the nutritive cells) leads them in the direction of the ovary. Once the pollen tubes are started in this direction there is usually nothing to reverse their orientation, but within the ovary, we find that the path followed becomes very devious and irregular. (We have successfully dissected the entire conducting tissue from the pistil, removing the ovules which remained attached to the dissection by their pollen tubes.) If the ovules in the path of a particular pollen tube have been previously fertilized, and it happens to find its way back to the conducting tissue through which it entered, it may emerge from the ovary and continue its growth toward the stigma. Of course, these observations do not necessarily deny the existence of chemotropism at the time a pollen tube enters the micropyle.

SPLICING OF STYLES IN CUT FLOWERS

Our experiments, in which we spliced styles on cut flowers which were kept in the laboratory, revealed some very interesting features. We found that when the parts of two different styles were joined perfectly in square joints, properly protected, and held in this position, many pollen tubes could pass across the wounded area. When the styles were not perfectly joined, the ends of the pollen tubes would enlarge considerably and extend themselves slightly beyond the conducting tissue as they were stopped. Figure 1 is taken from one of our laboratory tests, and shows the

behavior of pollen tubes at the joint between two styles. This figure is from a camera drawing of a selected part of this region and the conducting tissue is only schematically represented. The pollen tubes shown at the left had little difficulty in passing through the wounded area; those shown at the right were held in check by the gap at this point between the two neighboring conducting tissues. Some of the pollen tubes were attempting to cross the barrier and the figure shows how they may crowd up to and extend themselves beyond the extreme end of the upper cut surface. With the first tubes as support, others may extend themselves farther and
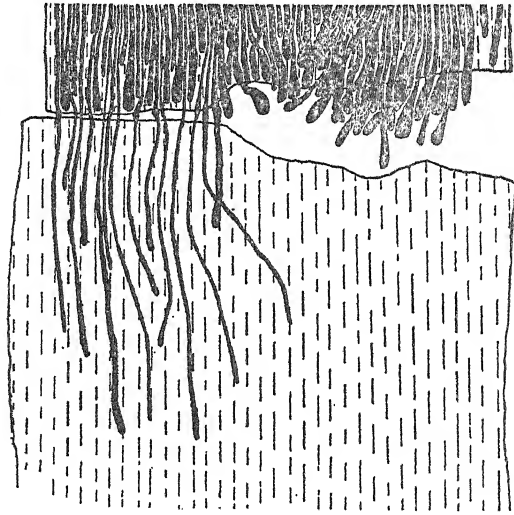
Fig. 1.

farther. Thus it could be observed in many instances that when crowded, a few of the pollen tubes may somtimes actually find their way across a considerable space to the nourishing tissue beyond the gap and continue their growth to the ovary.

These observations demonstrated the importance of obtaining a perfect union of the two strands of conducting tissue in the styles which are spliced. Though some pollen tubes are held in check at the joint, we counted hundreds of pollen tubes in our test slides which successfully passed over into the second style. We were, therefore, encouraged to make attempts to obtain seed capsules from such pollinations.

BI-MODAL DISTRIBUTIONS OF POLLEN TUBES

The conditions under which it may be desirable to splice a style are illustrated by the pollen tube distributions shown in figures 2 and 3. Here we find the pollen tube population, growing under favorable conditions,

and resolved into two groups. Only the ends of the pollen tubes were counted and plotted in their appropriate interval as they were growing from the stigma at the left toward the ovary at the right. Burst pollen tubes are plotted below the datum line and any ungerminated pollen grains are shown by the vertical bar at the left. Figure 2 shows a test using a moderate amount of the pollen of an F_2 plant derived from irradiation experiments. The bi-modal distribution is due to a gene which is recessive in the sporophyte carrier. Genes of this type are usually transmitted through half of the eggs, giving very satisfactory 1:1 ratios. Half of the male gametophytes also receive the gene which retards their growth. The group of long pollen tubes are growing at the same rate as those obtained from the pollen of normal plants. Their arrival in the ovary several hours before the second group, may enable them to monopolize the ovules
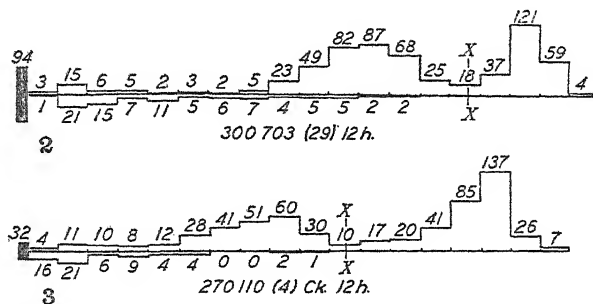
Figs. 2 and 3.

and leave none to be fertilized by the second group of pollen tubes which, therefore, may appear not to be transmitted through the pollen in ordinary pollinations. Since the pollen tubes in the longer group could only contribute the dominant allelomorph of this gene upon fertilization it is desirable to eliminate this group entirely and obtain a result similar to a back cross to the recessive, if this plant is selfed.

Likewise, in figure 3 from the pollen of one of the 25-chromosome plants where an extra chromosome is carried in the slow-growing half of the pollen tube population, we may wish to eliminate the longer pollen tubes which do not carry the extra chromosome. Since an extra chromosome behaves as a dominant character in heredity we may expect to approach 100 per cent transmission of this condition, if the fast growing pollen tubes are eliminated.

METHOD OF SPLICING STYLES

The splicing of styles on plants growing out of doors was most successful when done at night. The method which was finally elaborated is illustrated by steps in A-J, in figure 4.

Healthy, cut flowers from normal plants were pollinated under controlled conditions. Pollen was used which was known to give a bi-modal distribution of tubes. After sufficient growth had been attained to separate the two groups (8–12 hours at 18–20 degrees C.), one or more styles were killed, dissected, and stained as rapidly as possible (at least 30 minutes required). When properly stained, the condition of the tubes and the position of the two modes were determined by actual measurements. The distance from the stigma to the low point X between the two modes was measured and marked with parallel lines on a wooden gauge. This gauge
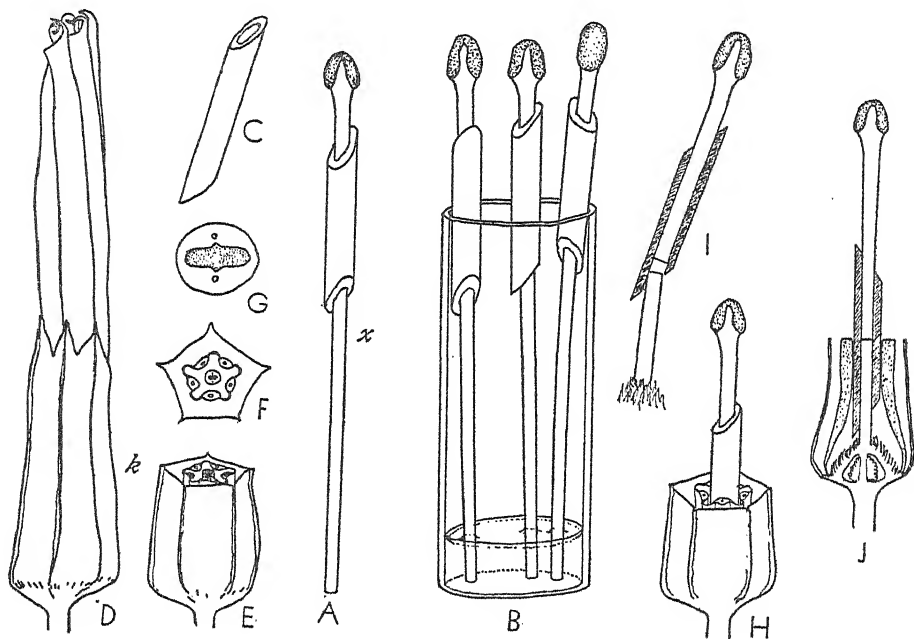
Fig. 4.

served as a guide in cutting the styles in the field. While the test slide and gauge were in process of preparation, the styles were removed from the remaining flowers and inserted into previously selected, closely-fitting grass straws C, as shown at A (the living culms of *Digitaria sanguinalis* were used). These were immediately set in vials containing a small quantity of water (fig. 4B) and transported to the field in this condition.

All the paraphernalia required for the field work *must be prepared in advance*, for speed and accuracy may determine the difference between success and failure. The following equipment is needed:

(1) Suitable tags showing pollination legends.

(2) A hunter's headlamp for each operator. These free both hands for

work and give a narrow beam of intense light which is necessary for the rather delicate manipulations.

(3) A sharp razor for each operator.

(4) A wooden gauge as described above, marked in such a way as to enable one of the operators to cut the style quickly, squarely and at the desired point corresponding to the low place (X) between the two modes shown in figs. 2 and 3.

(5) A small portable stool or table for instruments and material.

On the plant which is to serve as maternal parent a nearly mature, unopened bud is selected, one whose pollen has not been shed, such as is shown at D. At the point k, the fluted inner surface of the corolla is found to be constricted as shown in figure 4 at E and F. This constriction furnishes a natural clamp for holding the straw splint in place, as shown in position at H. For this reason the point k is selected and cut by one operator. At the same time the other operator places a style on his gauge and makes a clean square cut at the predetermined desired distance from the stigma and then discards the lower part of the style together with its contained tubes. The stigmatic portion together with its slow-growing tubes is retained and its newly cut surface drawn up into the body of the splint as seen at I. The straw is then carefully lowered over the newly cut end of the lower style which remains on the plant, as shown at I, H and J. The instant that the two cut surfaces come in contact further lowering of the straw thrusts upward the part bearing the stigma. Thus one may know when contact is made and the process is complete. If this operation is carefully carried out on field plants and then left undisturbed for a period of 10–12 hours, a sufficient number of fertilizations may be accomplished to cause a fruit to set. It is usually a small one, especially if the fast-growing tubes have been discarded, but contains sufficient seed to give as large a culture as one usually wishes to plant.

PRECAUTIONS

For the greatest success, certain precautions should be borne in mind. (1) General growth conditions and fruit setting should be good. (2) A rather high degree of atmospheric humidity is also necessary because otherwise the cut surfaces dry quickly and stop the passage of tubes. For this reason, we worked at night after the air approached the dew point. In damp weather, the operations can be performed in the evening thus taking advantage of twilight. (3) As will be seen from the cross section of the style G, fig. 4, the strand of conducting tissue is not circular, but elongated in cross section. If the two abutting strands are properly orientated, a perfect union is made, otherwise many tubes will be stopped be-

cause they find no continuity of conducting tissue at this point. In practice, this structural difficulty can be only partly overcome. (4) The straw splints, C should be obtained from living plants, and carefully selected to fit the style very closely. Diagonally cut ends will facilitate their insertion.

This method should not be called grafting. The tissues of a style are mature and do not unite by meristematic growth. They are merely brought closely together and held in place. If the splicing has been successful we estimate that the pollen tubes usually cross the joint within a 5–9 hour period following the operation. The pollen tubes actually serve as a bond to hold the united parts together, but the upper part of the joined style frequently dries out long before the lower portion, showing that no actual organic union of the stylar tissues occurs.

SEEDS FROM SPLICED STYLES

Our first attempts in splicing the styles on garden plants were made with normal pollen. We were naturally interested in demonstrating the possibility of obtaining successful fertilization by this method regardless of pollen tube distributions. In some cases, we cut off only a portion of the longest pollen tubes or made our incision in front of all of them. The seed capsules from 15 successful trials contained from 5–175 seeds, an average of 72. In another set of trials, we obtained from our successful attempts from 50–275 seeds, an average of 120. In a set of experiments using the pollen of (2n+1) Globes, we obtained 7 capsules ranging from 35–175 seeds with an average of 100.

We have now made a total of 50 successful pollinations with spliced styles. Many of these are from crosses in which the desired phenotypes would not appear in ordinary pollinations. The latter have not been planted as this is written. From the last series, the ovaries which dropped without setting fruits were collected and dissected. These yielded some valuable data concerning the minimum number of fertilizations required in an ovary to ensure a reasonable probability of a set. We found that 36 had no ovules fertilized, 15 had between 1 and 10 fertilizations, 15 had 11–20 enlarged ovules and 2 others between 21 and 30. Among the successful sets there were no capsules with less than 10 seeds, 3 with 11–20, 2 with 21–30, 5 with 31–50 and 13 with from 51–140 seeds each. Thus it appears that a minimum of about 20–30 ovules should be fertilized in order to ensure the setting of seed capsules in field-grown plants at times when the conditions of fruit setting are favorable.

Some of the crosses Normal X (2n+1) Globe were planted in order to test the Globe-transmission through the pollen by this method. Though the highest had only 31 per cent Globes, which is fewer than we might

expect to obtain, this is about a 15-fold increase over Globe-transmission in ordinary pollinations, and demonstrated that the 13-chromosome gametophyte of this mutant could be successfully transmitted by the method of splicing styles. Evidently we had placed our incision too far forward, thus including a majority of 12-chromosome pollen tubes. In our later experiments, in which the place of incision was determined with greater accuracy, so that more of the longer pollen tubes were discarded, the proportion of the progeny especially desired was much higher, in spite of the fact that the average number of seeds obtained was lower.

PROGENY TESTS AFTER STYLE-SPLICING

TABLE 1

	PLANTING NUMBER	PLANTS FROM FIRST OR LONGEST POLLEN TUBES NO.	PLANTS FROM SECOND GROUP OF POLLEN TUBES NO.	%	TOTAL PLANTS RECORDED HALF CAPS	WHOLE CAPS	PER CENT FROM 2ND GROUP OF POLLEN TUBES
Controls—Double pollinations, styles not spliced	U½ 31737	189	25	11.7	214	400	25.0
	L½ 31738	111	75	40.3	186		
	U½ 31739	201	10	5.0	211	440	19.1
	L½ 31740	155	74	32.3	229		
	U½ 31742	236	1	0.4	237	510	3.3
	L½ 31743	257	16	6.2	273		
	U½ 31748	200	2	1.0	202	388	12.0
	L½ 31747	139	47	25.3	186		
					Average for Controls		14.8
Tests—Double pollinations, styles spliced, discarding longest pollen tubes	U½ 31744	4	20	83.3	24	54	85.1
	L½ 31745	4	26	86.6	30		
	U½ 31749	1	35	97.2	36	62	74.2
	L½ 31750	15	11	42.3	26		
	31736	15	25			40	62.5
	31741	3	47			50	94.0
	31746	7	27			34	79.4
	31751	5	49			54	90.7
	31753	2	17			19	89.4
	31754	1	9			10	90.0
	31755	5	25			30	83.3
					Average		83.2
	31752*	25	4			29	13.2

* Style was cut too far foward, including longest group of pollen tubes.

In order to test the possibilities of this technique with distinct bimodal distributions of pollen tubes, we made some double pollinations using pollen which was known to give only a single mode of distribution from each separate pollination. The two pollinations were separated by an interval of four hours thus giving two modes. By using the pollen of the dominant gene for purple flowers and seedlings in one pollination, and the pollen from white plants in the other, and splicing these onto the flowers of white plants, we could tell from the color of the seedlings whether the desired group of longer pollen tubes had been excised. Table 1 gives the results of these tests together with similarly pollinated control-flowers which were not spliced.

The first four pollinations given in table I were some of our controls, and were divided into pedigrees representing seeds from the upper and lower half of the seed capsules. It is obvious that the pollen tubes of the second pollination (which were largely excised in treated styles) were almost completely excluded from the upper half of the seed capsules, but fertilized ovules in the lower portion to a much greater extent. The average for the entire capsules in the controls was about 15 per cent.

In our splicing tests the proportions obtained from the second pollination ranged between 62.5 and 94 per cent, with an average of 83.2 per cent. This is nearly a six-fold increase over the controls. However, one case (Planting #31752 listed at the bottom of this table) gave practically the same results as the unspliced controls. In this case, there can be little doubt that the incision was made too far forward, thus including all or nearly all of the longest group of pollen tubes. This serves to demonstrate the importance of knowing accurately the point X (see figures 2, 3 and 4A) at which the incision is to be made in order to discard the longest group of pollen tubes. On the whole, these genetic tests indicate that the method of splicing styles is practical, and may be expected to give greatly increased yields of zygotes coming from slow-growing pollen tubes.

The genetics of Neurospora—II. Segregation of the sex factors in asci of N. crassa, N. sitophila, and N. tetrasperma

CARL C. LINDEGREN

(WITH FIVE TEXT FIGURES)

Dodge (1927) has pointed out some of the advantages of the ascomycetes for studying meiosis. The primary nucleus of the ascus is formed by the fusion of two nuclei. The cell containing this nucleus gives rise to the ascus which is often long and tube-like. This nucleus then divides three times to form eight nuclei. Each of the eight spores receives one of these eight nuclei. In *Neurospora crassa* and *N. sitophila* an ascospore on germination gives rise to a mycelium, which may be of either one of the two sexes. Such a mycelium, usually called a 'haploid' mycelium, is sterile when grown alone or with another of the same sex, but, when the mycelia of two opposite sexes grow together, zygotes and ascospores are produced.

SEX AND ARRANGEMENT OF SPORES IN THE ASCUS OF NEUROSPORA CRASSA

In the two species mentioned, the tube-like ascus is long and narrow. Wilcox (1928) has studied the spindles in the ascus of *N. sitophila* and has found that, in the first two divisions, they are oriented parallel to the sides of the ascus and do not overlap. The nuclei maintain their relative order and positions. This means that it is possible, as shown in text figure 1, to determine at which division segregation of factors has taken place. This is done by studying the characters of the mycelia grown from the respective ascospores of a single ascus in which the position of the spores in the ascus is known. Text figure 1 shows three of the six possibilities for first- versus second-division segregation. The other three are represented by reversing the positions of the two kinds of nuclei. In text figure 1, a, showing first-division segregation, the upper four nuclei would be 'white' and the lower four 'black'.

Dodge (1929b) and Wilcox (1928) have shown in *Neurospora sitophila* that the factors for cultural characters and the factors determining the two sexes can be segregated at either the first or at the second division in the ascus. Dodge (1927) presented cytological evidence that in *N. tetrasperma*, a species containing four bisexual spores, where there is a very complex series of changes in spindle orientation, there is a greater probability of the sex factors being segregated at the first division than at the second. He also points out that the sex factors might be segregated at any one of the three divisions and still give rise to four bisexual spores. He studied the segregation of the sex factors in *N. crassa* (1930, 1931), and

stated that they were segregated at the first division in this species. By means of the arrangement of the spores in the long narrow ascus, the writer has also studied the segregation of the factors for the two sexes and for various pairs of cultural characters in *N. crassa*. Segregation was found not to occur at the third division, since, for all characters, the spores were found grouped as four pairs of identical twins. Dodge's study of the orientation of the spindles in this species shows that it is probably identical with that of *N. sitophila*. All of the asci, from which eight spores germinated, showed four spores of one sex and four of the opposite sex. The possible

a 　　　　　　　　 b 　　　　　　　　 c
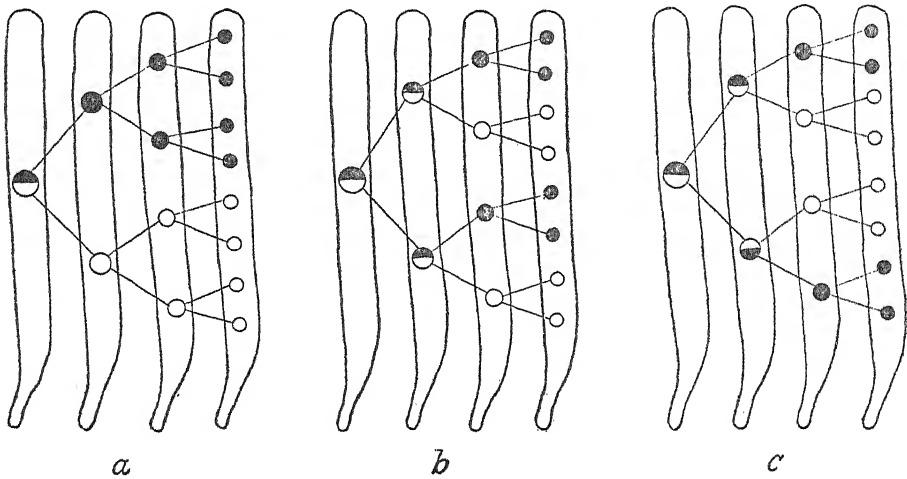
Fig. 1. a. Diagram of the arrangement of spores of opposite sex in the ascus of *N. crassa* that would result from segregation of the sex factors at the first division in the ascus, provided there was no passage of nuclei in the ascus. Black and white are used to designate the factors for the opposite sexes. The only variation of this arrangement that has been detected is a shift in the fourth and fifth place, giving three black, one white, one black, and three white nuclei. But this shift is rather infrequent. The second obvious possibility of a first-division segregation would result from the opposite orientation of the tetrad in the first division. The second ascus would then show a white nucleus above and a black one below, and the final arrangement in the ascus would be reversed. b. Diagram showing the arrangement of spores of opposite sex in the ascus that would result from a segregation of the factors for sex at the second division in the ascus and a failure to segregate them at the first division. A second possibility would result from changing the orientation of both nuclei in the binucleate stage. In this case, the last figure would show, from top to bottom, two white, two black, two white, and two black. Ascus 348 is an example of a shift in positions 2 and 3, following this type of segregation. c. Diagram of another arrangement of spores of opposite sex in the ascus of *N. crassa*, which would result from a second-division segregation of the factors for sex. If both nuclei in the binucleate stage were reversed, another possibility would be obtained with the four black nuclei in the center and two white at each end. Ascus 301 shows the change in this arrangement resulting from a one place shift.

arrangements in an ascus for eight spores, four of one sex and four of the opposite sex, are seventy. This is given by the formula:

$$\frac{8!}{4!\times 4!}=70$$

Table 1 shows 32 of the asymmetrical and the 6 symmetrical permutations.

TABLE 1

Permutations of ascospores in the ascus

			32 OF THE ASYMMETRICAL PERMUTATIONS				
SPORE 1	2	3	4	5	6	7	8
+	+	+	+	−	−	−	−
+	+	+	−	+	−	−	−
+	+	+	−	−	+	−	−
+	+	+	−	−	−	+	−
+	+	+	−	−	−	−	+
+	+	−	+	+	−	−	−
+	+	−	−	+	+	−	−
+	+	−	−	−	+	+	−
+	+	−	+	−	+	−	−
+	+	−	−	+	−	+	−
+	+	−	−	−	+	−	+
+	+	−	+	−	−	+	−
+	+	−	−	+	−	−	+
+	+	−	+	−	−	−	+
+	−	+	+	−	−	−	+
+	−	−	+	−	+	−	+
+	−	−	−	+	+	−	+
+	−	+	−	+	−	−	+
+	−	+	−	+	−	+	−
+	−	−	−	+	+	+	−
+	−	−	+	+	+	−	−
+	−	+	−	−	+	+	−
+	−	−	+	−	+	+	−
+	−	+	+	−	+	−	−
+	−	+	+	+	−	−	−
+	−	+	−	+	+	−	−
+	−	−	+	+	+	−	−
+	−	+	+	−	−	+	−
−	−	+	+	−	+	+	−
−	−	+	+	+	−	+	−
−	−	+	−	+	+	+	−
−	−	−	+	+	+	+	−
			THE 6 SYMMETRICAL PERMUTATIONS				
+	+	−	−	−	−	+	+
−	−	+	+	+	+	−	−
+	−	+	−	−	+	−	+
−	+	−	+	+	−	+	−
+	−	−	+	+	−	−	+
−	+	+	−	−	+	+	−

The remaining 32 asymmetrical permutations are obtained by an end to end reversion of the 32 asymmetrical ones shown. If the arrangement of spores in the ascus is determined by pure chance, there is one chance in 70 of each such permutation occurring.

The six arrangements, of which three are shown in text figure 1, could all be the result of either first- or second-division segregation, provided the spindles in the second division were long enough and the ascus wide enough to permit the two middle nuclei to pass each other in the four-nucleate stage, as is the case in *N. tetrasperma*. Text figure 2, a is a diagram showing such a shift in position. With such a shift, a first-division segregation would produce the arrangement usually ascribed to second-division segregation and vice versa. If such a shifting occurred, it might be ob-

a   b   c
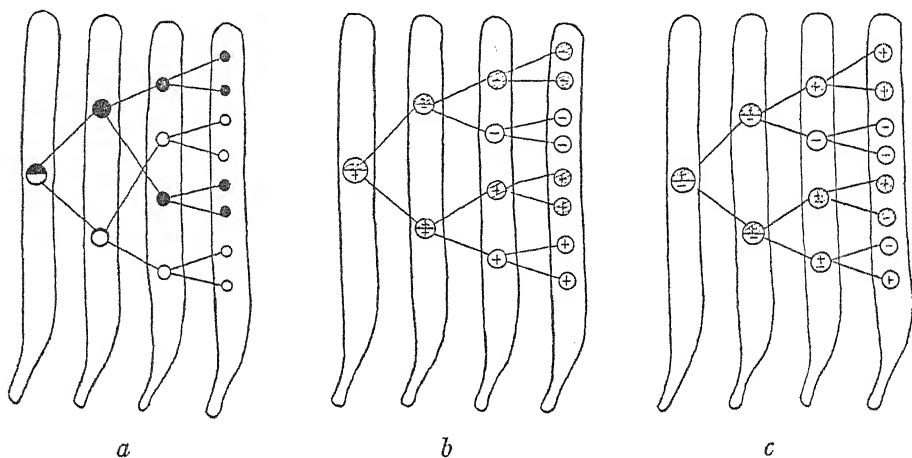
Fig. 2. a. Diagram showing how the transposing of the second and third nuclei in the four-nucleate stage would result in first-division segregation producing the arrangement of spores ascribed to second-division segregation and vice versa. The cytological evidence of Wilcox and Dodge show this to be highly improbable. b. Diagram of the arrangement of the spores of opposite sex and producing tan and wild-type mycelia in ascus 114. Diagonally lined nuclei are wild-type and open nuclei are tan. This arrangement of spores proves that, even if a shift as shown in figure 2,a had taken place, both first- and second-division segregation occurred. c. Diagram of a hypothetical ascus showing an arrangement of spores of opposite sex and different cultural characters that would prove that third-division segregation had occurred. No such ascus has been found.

jected that the data do not show evidence of more than one type of segregation. But Wilcox (1928), in her cytological study of a closely related species, *N. sitophila*, shows that no such shifting takes place. Moreover, ascus 114 (text fig. 2, b) proves that both first- and second-division segregations occur. A character, which was called tan, appeared in the mycelia

grown from the ascospores of this ascus. The conidia of tan were produced more sparsely than in the wild-type, and were white or yellow, while those of the wild-type were orange or light orange. In text figure 2, b, it can be seen that the sex factors were segregated at the first division, while wild and tan were segregated at the second. Even if it were assumed that the second and third nuclei exchanged positions after the second division, the results show that both first- and second-division segregations must have taken place.

Table 2 is a record of the sex and arrangement of the ascospores in 275 asci of *N. crassa*, comprising six generations. These asci are all descended from a single ascus. In each column, the numbers at the left are the numbers of the individual asci. The plus sign indicates that the mycelium of the respective ascospore produced fertile perithecia when mated to a tester strain. The minus sign indicates that no perithecia were produced by a similar mating. The plus sign indicates that the ascospore is opposite in sex to the tester strain, and the minus sign indicates that it is the same sex. The eight spaces from left to right correspond to the positions of the ascospores in the ascus. The first position indicates the ascospore located at the tip of the ascus and the eighth position indicates the ascospore located at the base. A bracket at the left of the numbers of the asci indicates that all of the asci bracketed come from one perithecium and the number at the left of the bracket is the number of the perithecium. Above each group is shown the mating which produced the corresponding asci. For example 0–1×6–2 means mating the mycelium from the first ascospore in ascus 0 to the mycelium from the second ascospore in ascus 6. The symbols I×I following indicate that ascus 0 was an ascus in which the sex factors were segregated at the first division in the ascus, and ascus 6 was an ascus in which the sex factors were also segregated at the first division. Roman numeral II is the symbol used to indicate second-division segregation of the sex factors.

When a spore does not germinate its position is indicated by a circle. When it is possible from the position and sex of the other spores to determine the sex of the missing spore, a plus or minus sign is placed within the circle. From the fact that, in every case where all eight spores germinated, there were four of one sex and four of the opposite sex in the ascus, this determination is easy to make.

The arrangement of the spores in the asci shows that segregation of factors determining sex may occur either at the first or the second division in the ascus. Exceptional asci are marked by parentheses. These undoubtedly are all due to slipping of adjacent nuclei past each other during or after the third division. Rough handling in dissection might cause shifting of

TABLE 2

Sex and arrangement of ascospores in 275 asci of Neurospora crassa.

P₃ Generation

```
Ascus
    0    − − − − + + + +
```

P₂ Generation (0–1×0–8) I selfed

```
Ascus                          Ascus
  (1)ᵃ  − − + + + − − +          6    + + + + − − − −
    2   − − + + + ⊕ − −          7    ⊕ + + + − − − −
    4   − − − ⊖ + + + +        (10)ᵃ  ○ − − + + ○ − ○
    5   + + + ⊕ − − ⊖ −
```

4 I:2 II; 1 (?)

Back Cross Generation P₂×P₃

```
(0−1×6−2)I×I                        (0−1×7−3)I×I
Ascus                               Ascus
    113  − ⊖ + ⊕ + + − −        137 ⎰ 137  − − − − + + ⊕ +
    114  − − − − + + + +            ⎱ 139  − − − − + + + +
    116  + + − − − − + +              141  − − − − + + +−+
    118  + + + ⊕ − − − −              142  + + − − − − + ⊕
    120  + + − − + − − −              144  ⊖ ⊖ − − + + + +
    122  − − − − + + + +                        4 I:1 II
    123  − − − − + + + ⊕
  ⎧ 124  ⊕ + + + − − − −        (0−1×10−4)I×II (?)
  ⎪ 126  + + + + − − − −        Ascus
  ⎪ 125  − − − − + + + +            106  + + + + − − − −
  ⎪ 127  + + + + − − − −            107  − − − − + + + +
  ⎪ 128  + + + + − − − −          (109)ᵃ − − − ⊕ − + + +
124⎨ 129  + + + + − − − −            110  − − + + − − + ⊕
  ⎪ 130  + + + + − − − −            112  + + + + − − − −
  ⎪ 131  − − − − + + + +                      4 I:1 II
  ⎪ 132  + + + + − − − −
  ⎪ 133  + + + + − − − ⊖        (0−1×1−3)I×II (?)
  ⎪ 134  + + + + − − − −        Ascus
  ⎩ 136  + + − − − − + +            100  ⊖ − − − + ⊕ + +
         15 I:4 II                 101  − − + + + + ⊖ ⊖
                                   103  − − − − ⊕ + + +
                                   104  + ⊕ ⊕ + − − − −
                                             3 I:1 II
```

ᵃ The parentheses enclosing the ascus number throughout this table indicate that a shift of the nuclei, after the third division, may have occurred or the spores were misplaced in the manipulation.

P₁ Generation (4−5×6−5)I×I

```
Ascus                          Ascus
   299  ⊕ + + + − − − −          306  − − − − + + + +
  (301) + − + − − − + +          308  + + + + − − − −
   302  − ⊖ − − + + + +          314  + + + ⊕ − − − −
   303  + + + + − − − −          316  − − − − + + + +
```

P_1 Generation $(4-5 \times 6-5) I \times I$ (*continued*)

Ascus									Ascus								
317	+	+	+	+	−	−	−	−	323	+	+	−	−	−	−	+	+
318	+	+	+	+	−	−	−	−	(324)	−	−	−	+	−	+	+	+
320	−	−	−	−	+	+	+	+	325	−	−	−	−	+	+	+	+
322	−	−	−	−	+	+	+	+	329	−	−	−	−	+	+	+	+

14 I:2 II

F_1 Generation (Ascus 114 selfed) I selfed

$(114-1 \times 8)$ I selfed

158	+	+	+	+	−	−	⊖	−
159	+	+	+	+	−	−	⊖	−
160	+	+	+	+	−	−	−	−
164	⊕	⊕	+	+	−	−	−	−

4 I:0 II

$(114-1 \times 7)$ I selfed

Ascus										Ascus									
	216	−	−	−	−	+	+	⊕	⊕		254	−	−	+	+	+	+	−	−
	217	−	−	−	−	+	+	⊕	+		255	−	⊖	−	−	+	+	+	+
	218	+	+	+	+	−	−	−	−		257	+	+	+	+	−	−	⊖	−
	219	+	+	+	+	−	−	−	−	258	258	+	+	+	+	−	−	−	−
	(220)	−	−	−	+	−	+	+	+		259	−	−	−	−	+	+	+	+
218	221	+	⊕	+	+	⊖	−	−	−		263	−	−	−	−	+	+	+	+
	222	+	⊕	⊖	−	+	+	−	−		264	−	−	−	−	+	+	+	+
	223	−	−	−	−	+	+	+	+		265	−	−	−	−	⊕	+	+	+
	225	+	+	+	+	−	−	−	−	260	266	+	+	+	+	−	−	−	−
	(226)	+	+	+	−	+	−	−	−		267	+	+	+	+	−	−	−	−
	224	−	⊖	−	−	+	+	⊕	+		268	−	−	−	−	+	⊕	+	+
	227	⊕	+	+	+	−	⊖	−	−		271	−	−	−	−	+	+	+	+
228	228	−	−	−	−	+	+	+	+		273	+	+	+	⊕	−	−	⊖	⊖
	229	+	+	+	+	−	−	−	−		274	−	−	−	−	+	+	+	+
230	230	−	−	−	−	+	+	+	+	275	275	−	−	−	−	+	+	+	+
	231	−	−	+	+	+	+	−	−		276	−	−	−	−	+	+	+	+
	232	−	−	−	−	+	⊕	+	+	277	277	+	+	+	+	−	−	−	−
	233	−	−	−	−	+	+	+	+		278	+	+	+	+	−	−	−	−
	234	+	+	−	−	+	+	−	−		280	+	+	−	⊖	−	−	+	+
233	(235)	+	+	+	−	+	−	−	−	281	281	−	−	−	−	+	+	+	+
	236	−	−	−	−	+	+	+	+		282	+	+	+	+	−	−	−	−
	237	+	+	+	+	−	−	−	−	284	284	+	⊕	+	+	−	−	−	⊖
	238	−	−	−	−	+	+	+	+		285	⊖	−	−	−	+	+	⊕	+
239	239	+	+	−	−	+	+	−	−		286	−	−	−	−	⊕	+	+	+
	240	−	−	−	−	+	+	+	+		288	−	−	−	−	+	+	⊕	+
	242	+	+	+	+	−	−	−	−		289	+	+	−	−	−	−	+	+
243	243	−	−	−	−	+	+	+	+		290	⊕	⊕	−	−	⊕	+	−	−
	244	+	+	+	+	−	−	−	−	291	291	−	−	−	−	+	+	+	+
248	248	−	−	−	−	+	⊕	+	+		292	+	+	+	+	−	−	−	−
	249	−	−	−	−	⊕	+	+	+											
	251	−	−	−	−	+	⊕	+	⊕											
251	252	+	+	−	−	−	−	+	⊕											
	253	+	+	+	+	−	−	−	−											

53 I:9 II

TABLE 2 *(continued)*

F_2 Generation

(223−1×230−6)I×I

Ascus

331	−	−	−	−	+	⊕	+	+
332	+	+	⊕	+	−	−	⊖	−
333	+	+	⊕	+	−	⊖	−	−
335 { 335	−	−	−	−	+	+	+	+
336	−	−	+	+	+	+	⊖	−
337	+	+	−	−	−	−	+	+
338	−	−	+	+	+	+	−	−
339	−	−	−	⊖	+	+	⊕	⊕
340	⊕	+	+	+	−	−	−	−
341	+	+	+	+	−	−	−	−
343	⊕	+	+	+	−	−	−	−

8 I:3 II

(223−7×229−8)I×I

Ascus

345	−	−	−	−	+	+	+	+
346	−	−	−	−	+	+	+	+
347	+	+	+	+	⊖	−	−	−
349 { (348)	+	−	+	−	+	+	+	+
(349)	−	−	⊖	+	−	+	+	+
350	+	+	+	+	−	−	−	−
351	+	+	−	−	−	−	+	+
352	−	−	−	−	+	+	+	+
353	−	−	−	−	+	+	+	+
354	⊖	−	⊖	−	+	+	+	+
355	+	+	+	+	−	−	−	−
356	−	−	⊖	−	+	+	+	+
357	−	−	−	−	+	+	+	+
358	⊕	+	+	+	−	−	−	−
359	−	−	−	−	+	+	+	+
360	−	−	+	+	+	+	−	−
362	−	−	−	−	+	⊕	+	⊕

14 I:3 II

(160−1×8)I selfed

Ascus

(493)	⊖	−	−	+	−	+	+	+
494	−	−	−	−	+	+	+	⊕
496	−	−	⊖	⊖	⊕	+	+	+
498	⊖	−	−	−	+	⊕	+	+
500	−	−	−	−	+	+	+	+
502	+	+	⊕	+	−	−	−	−
503	+	+	+	+	−	−	−	−
504 { 504	+	+	+	+	−	−	−	−
505	−	−	−	−	+	+	+	+
506	⊕	+	−	−	+	+	−	−
507	−	−	−	−	+	⊕	+	+
508	−	−	−	−	+	+	+	+
509 { 509	+	+	+	+	−	−	⊖	−
510	+	+	+	+	−	−	−	⊖
511	⊖	−	⊖	−	+	+	+	+
512	−	−	−	−	+	+	+	+
513	+	+	+	+	−	−	−	−
514	+	+	+	+	−	−	−	−
515	+	+	+	+	−	−	−	−
517 { 518	⊕	+	+	+	−	−	−	⊖
519	−	−	−	−	+	+	+	+
520	−	−	−	−	⊕	+	+	+

21 I:1 II

(226−1×6) I selfed

Ascus

450	+	⊕	+	+	−	−	−	−
452	+	+	+	+	⊖	⊖	−	−
453	+	+	+	+	−	−	−	−
459	+	+	+	⊕	⊖	−	−	−
466	+	+	+	+	−	⊖	−	−
467	+	+	+	+	−	−	−	⊖

6 I:0 II

F_2 Generation

(243−2×5) I selfed

Ascus

364 { 364	−	−	−	−	+	+	+	+
365	+	+	+	+	−	−	−	−
366	−	−	−	−	+	+	+	+
367	−	−	−	−	+	+	+	+
368	+	+	−	−	+	+	−	−
369	−	−	−	−	+	+	+	+
370	−	−	+	+	−	−	+	+
372	+	+	+	+	−	−	−	−

Ascus

373 { 373	−	−	−	−	+	+	+	+
374	+	+	+	+	−	−	−	−
375	−	−	−	−	+	+	+	+
376	−	−	−	−	+	⊕	+	+
377	−	−	−	−	+	+	+	+
(378)	−	−	−	+	−	+	+	+

12 I:2 II

(273−3×290−3) I×II

569 {	569	−	−	−	−	⊕	+	⊕	+
	570	+	+	+	+	−	−	−	−
571 {	571	+	+	−	−	+	+	−	−
	572	+	+	+	+	−	⊖	−	−
573 {	573	−	−	−	−	+	⊕	⊕	+
	574	⊖	⊖	⊕	+	−	−	+	⊕
	575	⊕	+	+	⊕	⊖	⊖	−	−
	576	+	+	+	+	−	−	−	−
577 {	577	+	+	+	+	−	−	−	−
	578	−	−	−	−	+	+	+	+
	579	+	+	+	+	−	−	−	−
	580	−	−	−	−	+	+	+	+
581 {	581	−	−	−	−	+	+	+	+
	582	−	−	−	−	+	+	+	+
	583	−	−	−	−	+	+	+	+
583 {	584	+	+	+	+	−	−	−	⊖
	585	−	−	−	−	+	+	+	+

15 I:2 II

(288−5×290−7) I×II

546 {	548	−	−	−	−	⊕	+	+	+
	549	−	−	⊖	−	⊕	+	+	⊕
	550	−	−	+	+	+	+	−	−
551 {	551	−	−	⊖	⊖	+	+	+	+
	552	+	+	+	+	−	−	−	−
553 {	553	+	+	+	+	−	−	−	−
	554	+	+	+	+	−	−	−	−
	555	−	−	−	−	+	+	+	+
555 {	556	−	−	−	−	+	+	+	⊕
	557	−	−	−	−	+	+	+	+
558 {	558	+	+	+	+	−	−	−	−
	559	+	+	+	+	−	−	−	−
560 {	561	−	−	−	−	+	+	+	+
	562	−	−	−	⊖	+	+	+	+
	(564)	⊕	⊕	+	−	+	−	−	−
	567	−	−	−	−	+	+	+	+

15 I:1 II

F₃ Generation

(337−6×7) II selfed

Ascus

379	+	+	+	+	−	−	−	−
380	−	−	−	−	+	+	+	+
381	−	−	−	−	+	+	+	+
382	+	+	−	−	−	−	+	+
383	+	+	+	+	−	−	−	−
384	−	−	−	−	+	+	+	+

5 I:1 II

(337−2×3) II selfed

Ascus

385	−	−	+	+	+	+	⊖	−
386	+	+	+	+	⊖	−	−	−
387	−	−	−	−	+	+	+	+
388	−	−	+	+	+	+	−	−
389	−	−	−	−	+	+	+	+
390	−	−	−	−	+	⊕	+	+

4 I:2 II

(338−6×7) II selfed

Ascus

470 {	470	+	+	+	+	−	−	−	⊖
	471	−	−	−	⊖	+	+	+	+
473 {	473	−	−	−	⊖	+	+	+	+
	474	−	−	−	⊖	+	+	+	+
473 {	475	+	+	⊕	+	⊖	−	−	−
	476	+	+	+	+	−	−	⊖	−
477 {	477	−	−	−	−	+	+	+	⊕
	478	−	−	+	+	+	+	−	−
	479	⊕	⊕	+	+	−	−	−	−
480 {	480	−	−	−	−	+	+	+	+
	481	−	−	−	−	+	+	+	+
	482	−	−	+	+	+	+	−	−
	483	−	−	−	−	+	+	⊕	+
	484	−	−	⊖	−	+	+	+	+
486 {	486	−	−	−	−	+	+	+	+
	487	+	+	⊕	+	−	−	−	−
488 {	488	−	−	−	−	+	+	+	+
	489	−	−	−	⊖	+	+	+	+
	490	−	−	−	−	+	+	+	+

17 I:2 II

(338−2×3) II selfed

Ascus

	524	−	−	−	−	+	+	+	+
525 {	525	−	−	+	+	−	−	+	+
	526	+	+	+	+	−	−	−	−
	527	+	+	+	+	−	−	−	−
	528	−	−	−	−	+	+	+	+
528 {	529	−	−	−	−	+	+	+	+
	530	+	+	+	+	−	−	−	−
	531	+	+	+	+	−	−	−	−
532 {	532	⊖	−	+	+	−	−	+	+
	533	+	+	+	+	−	−	−	−
534 {	534	−	−	−	−	+	+	+	+
	535	+	+	+	+	−	−	−	−
	536	−	−	⊖	−	+	+	+	+
	537	+	+	+	+	−	−	−	−
540 {	540	+	+	+	⊕	−	−	−	−
	541	−	−	−	−	+	+	+	+
	543	⊖	−	⊕	+	+	+	−	⊖
	544	+	+	+	+	−	−	−	−

15 I:3 II

the ascospores. Ascus 226 is a case in point. The arrangement of the asco-spores of different sex, shown in table 2 (for ascus 226), indicates a shift in positions 4 and 5. The arrangement of the spores producing different types of mycelia as shown in table 3 confirms the fact that this is merely shifting of the nuclei. It is clear that tan and Normal factors are segregated independently of the sex factors, yet the same peculiar arrangement of the

TABLE 3

Sex and cultural characters of ascospores in Ascus 226.

ASCOSPORES	1	2	3	4	5	6	7	8
Sex............	+	+	+	−	+	−	−	−
Character.......	N	N	t	N	t	N	t	t

fourth and fifth spores in ascus 226 holds for the tan- and Normal-produc-ing spores as well as for the spores of opposite sex. Reversing the fourth and fifth spores, gives a simple first-division segregation of the sex factors and a second-division segregation of the factors for tan and Normal. Two other exceptions, which cannot be readily interpreted on this basis, are asci 1 and 10. These were dissected before the writer became expert enough to be certain of his technique.

To date no evidence has been obtained of segregation of any factors at the third division in the ascus. Text figure 2, c is a diagram of a hypo-thetical ascus, which would be evidence for a third-division segregation, if encountered. No such ascus has been discovered.

In order to facilitate discussion, from this point on, some abbreviations will be used. In making matings, individual ascospores were planted in separate tubes on nutrient agar until mycelia and conidia appeared. Then some of the mycelia and conidia from two tubes were planted into a third tube. Strictly speaking, of course, matings were made between clones pro-duced by ascospores, and not between the ascospores. However, from now on, such matings as that which produced the P_2 generation will be de-scribed as follows: Ascospore 0–1 was mated to ascospore 0–8, or, more briefly: 0–1 × 0–8 (I selfed). The expression in parentheses is a second con-vention indicating that the mating was made between mycelia produced by ascospores from the same ascus (selfed) and that segregation of the sex factors occurred at the first division (I).

Ascus 0, shown in table 2, is the parent ascus of all the *N. crassa* asco-spores studied. From the P_2 generation, which was produced by a I selfed mating (0–1 × 0–8), six asci were dissected. In four of these asci, the sex factors were segregated at the first division, and, in two of them, they

were segregated at the second division. Stated briefly: the P_2 generation produced by a I selfed mating contained four I and two II. This is 67 per cent I.

The four groups in the $P_2 \times P_3$ back-cross generation contained 79, 80, 80, and 75 per cent I respectively. The first two groups were produced by a I $\times$ I mating, and the second two groups by a I $\times$ II mating.

It is evident in this and the succeeding generations (perithecia 124, 218, 230, 233, 239, 251, and 277) that first- and second-division segregation of sex may occur in asci side by side in the same perithecium.

TABLE 4

Summary of table 2 showing the percentages of first-division segregation produced by twenty matings in seven generations.

GENERATION	TOTAL NO. OF ASCI	MATING	%-I
P_3	1		100
P_2	6	I selfed	67
$P_2 \times P_3$	19	I $\times$ I	79
$P_2 \times P_3$	5	I $\times$ I	80
$P_2 \times P_3$	5	I $\times$ II?	80
$P_2 \times P_3$	4	I $\times$ II?	75
P_1	16	I $\times$ I	88
F_1	62	I selfed	86
F_1	4	I selfed	100
F_2	11	I $\times$ I	73
F_2	17	I $\times$ I	82
F_2	22	I selfed	96
F_2	14	I selfed	86
F_2	6	I selfed	100
F_2	16	I $\times$ II	94
F_2	17	I $\times$ II	88
F_3	6	II selfed	83
F_3	19	II selfed	90
F_3	6	II selfed	67
F_3	18	II selfed	83
			MEAN 85%-I

Table 4 summarizes the data in table 2. It is apparent that the three types of matings. (I $\times$ I, I $\times$ II, and II $\times$ II) give approximately the same percentage of I. The mean of the total 275 asci is 85 per cent I, and the percentages obtained in the II $\times$ II matings vary no more from this mean than those obtained by the I $\times$ I matings.

Table 5 illustrates this point. All of the matings are grouped into their three different classes. I $\times$ I produced 85 per cent I; II $\times$ II produced 84 per cent I; and I $\times$ II produced 88 per cent I. In order to determine if the deviation of the I $\times$ II and the II $\times$ II matings from the I $\times$ I matings was

significant, the ratio of the deviation to the probable error was determined. Deviations were calculated from the 85 per cent obtained in the 182 I×I asci. It is obvious that this ratio is much less than 3, which is generally accepted as indicating significance.

TABLE 5

Data in table 4 arranged to show the percentage of first-division segregation produced by all the I×I I×II, and II×II matings.

MATING	NUMBER OF ASCI SHOWING FIRST-DIVISION SEGREGATION	NUMBER OF ASCI SHOWING SECOND-DIVISION SEGREGATION	PERCENTAGE OF FIRST-DIVISION SEGREGATION	$\dfrac{d}{P.E.}$
I×I	155	27	85	
I×II	37	5	88	.81
II×II	41	8	84	.30

The best test for the possibility of genic factors regulating the type of segregation is selection and subsequent crossing. Table 6 gives the results of six generations of selection for first-division segregation. It may be seen from the table that even after six generations of I×I matings, the percentage of first-division segregation is not increased.

TABLE 6

Results of selections for first-division segregation carried on through six generations.

GENERATION	NUMBER OF ASCI	PERCENTAGE OF FIRST-DIVISION SEGREGATION	MATING
P_3	1		
P_2	6	67	(0–1×0–8)(I selfed)
$P_{2×3}$	19	79	(0–1×6–2)(I×I)
P_1	16	88	(4–5×6–5)(I×I)
F_1	62	86	(114–1×7)(I selfed)
F_2	17	82	(223–7×229–8)(I×I)

Therefore, there is established this definitive numerical datum: The sex factors are segregated at the first division of the ascus nucleus in 85 per cent of the asci of *Neurospora crassa* and at the second division of the ascus nucleus in 15 per cent of the asci. This applies to the asci containing eight ripe spores. These percentages are constant regardless of whether the sex factors had been segregated at the first or second division in either or both parents. It is not possible by selection to increase or diminish these percentages. Thus the type of segregation obtained cannot be directly attributed to the effect of genic factors.

On the basis of pure chance, four types of II should occur with equal

frequency. Table 7 shows the frequency of each one of the four types encountered in the forty II obtained. There are 26 cases in which four like

TABLE 7

Frequency distribution of the four possible types of second-division segregation.

TYPE OF II	FREQUENCY
− − + + + + − −	16
+ + − − − − + +	10
+ + − − + + − −	9
− − + + − − + +	5

nuclei are grouped in the center of the ascus as compared with the 14 cases in which the like nuclei are arranged by twos in the ascus.

SEX AND ARRANGEMENT OF THE SPORES IN THE ASCUS
OF NEUROSPORA SITOPHILA

Fifteen asci of *N. sitophila*, from three consecutive generations, were studied. Table 8 shows the sex and arrangement of spores in these asci. From ascus 89, in which the sex factors had been segregated at the first

TABLE 8

Sex and arrangement of the ascospores in fifteen asci of N. sitophila.

First generation

Ascus
89   + + − − − − + +

Second Generation
89−1×4

Ascus
26   ⊖ ⊖ + + ⊖ ⊖ + ⊕
29   − − + ⊕ ⊕ + − −
30   ⊕ + + + ⊖ ⊖ − ⊖
31   ⊕ ⊕ + + ⊖ − ⊖ −
32   + + + ⊕ − ⊖ ⊖ ⊖
34   ⊖ ⊖ + ⊕ + + − −
35   + + + + − ⊖ ⊖ ⊖
40   ⊕ + + + − − − −
5 I:3 II

Third Generation
40−2×8

Ascus
203   + + + + − − − −
204   − − + + − − + +
205   + + + + − − − −
207   + + + + − − − −
209   + + − − + + − −
210   + + − − − − + +
3 I:3 II

division, a second generation was produced by mating the mycelia from the first and fourth ascospores. Eight asci from this generation were studied. In five of these asci the sex factors had been segregated at the first division, and in three of them they had been segregated at the second division in the ascus.

From ascus 40, in which the sex factors were segregated at the first division, a third generation was produced. In three of the third generation

asci, the sex factors were segregated at the first division, and in three others the sex factors were segregated at the second division.

In other words, matings between spores from an ascus in which the sex factors had been segregated at the first division produced both first- and second-division offspring. Moreover, matings between spores from an ascus in which the sex factors had been segregated at the second division also produced both first- and second-division offspring. This is in agreement with the data already reported in the case of *N. crassa*. An insufficient number of asci was tested to ascertain if the ratio of first- to second-division segregation was constant.

a   *b*
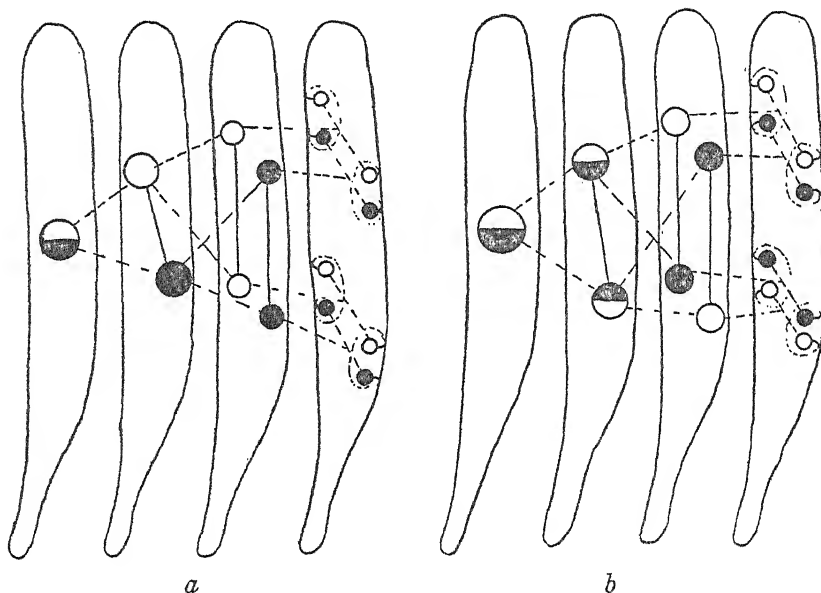
Fig. 3. a. Orientation of the spindles in the ascus of *N. tetrasperma*, as described by Dodge, and the resultant production of four bisexual spores following first-division segregation of the factors for sex. b. Diagram showing the orientation of nuclei necessary to produce four bisexual spores in the ascus of *N. tetrasperma*, following second-division segregation of the sex factors.

SEX AND ARRANGEMENT OF THE SPORES IN THE
ASCUS OF NEUROSPORA TETRASPERMA

Dodge (1927) has described very carefully the orientation of the spindles in the ascus of *N. tetrasperma*. Text figure 3 summarizes his findings. It is obvious that segregation of the sex factors at the first division in the ascus would invariably produce the four bisexual spores usually found. Text figure 3, b, shows that a second-division segregation of the sex factors could produce the same result if the tetrads in the binucleate stage were

oriented in the particular manner shown. Text figure 4 shows some of the possibilities if the tetrads were oriented in the opposite way.

Dodge has shown that not all of the asci of *N. tetrasperma* contain four spores. He has described many abnormal asci and found that the number of spores in an ascus may vary from one to six. The writer has also found asci containing seven and eight spores. Text figure 5 shows the sex and arrangement of the spores in 14 five- and six-spored asci. Large circles designate large spores and small circles designate small spores. Plus and minus signs indicate the respective sexes, while a circle containing both a plus and a minus sign indicates a bisexual spore. A question mark indicates that the respective spore did not germinate, and consequently its sex was not discovered. But it was occasionally possible to ascertain its sex from the known fact that four nuclei of each sex are formed in each ascus. In the case of asci 119 and 134, two alternative possibilities are suggested.

In the five-spored asci, the two small spores were of opposite sex. In asci 91, 97, and 106, these small spores were probably formed because the two adjacent nuclei of opposite sex were too far apart to be incorporated into a single spore. Each unisexual nucleus formed a spore wall about itself. Dodge's cytological work has shown that a beak is produced at the tip of each nucleus. This beak is curved at the end like an umbrella handle and probably has its origin in the central body or the astral rays. When the beaks of two adjacent nuclei are close enough together, these nuclei are included within a single large spore.

In asci 92, 98, 102, 107, 108, and 95, a different arrangement of the spores was found. The two small unisexual spores were separated by a single large bisexual spore. It appears that when the eight unisexual nuclei were formed in the ascus (see fig. 3, a), instead of unisexual nuclei 5 and 6 uniting to form the third bisexual spore, and unisexual nuclei 7 and 8 uniting to form the fourth bisexual spore, an unusual combination took place. In these cases, nuclei 6 and 7 were so placed that they were more easily incorporated into a single bisexual spore with each other than with their normal partners. This was probably because the two beaks were so situated with regard to each other that a single ascospore was cut out. This left nuclei 5 and 8 alone, and each made a single unisexual spore. The linear arrangement of the spores in the ascus, as a result of first-division segregation of the sex factors would result in nuclei 5 and 8 being of opposite sex. Nuclei 6 and 7 would also be of opposite sex and their incorporation into a single large spore would make a bisexual spore.

No explanation has yet been evolved for the fact that when a five-spored ascus of the type of ascus 92 is found, it is usually the nuclei at the base of the ascus that participate in the abnormal arrangement. Six-

spored asci 104 and 155 show that the upper four nuclei are capable of undergoing such an abnormal arrangement as well. Nuclei 2 and 3 (fig. 3,a), as well as nuclei 6 and 7, united to form bisexual spores, leaving unisexual nuclei 1, 4, 5, and 8 to form individual spores. The failure of nuclei 4 and 5 to form a single bisexual spore is interesting, for they are close to each other and of opposite sex. It is probably the orientation of the beaks which prevents the formation of a single bisexual spore in these cases. Text figure 3, a, shows that nuclei 4 and 5 are usually found with their beaks pointing in opposite directions. Each one cuts out a single unisexual spore. These findings confirm the view that opposite orientation of the beaks is a most im-
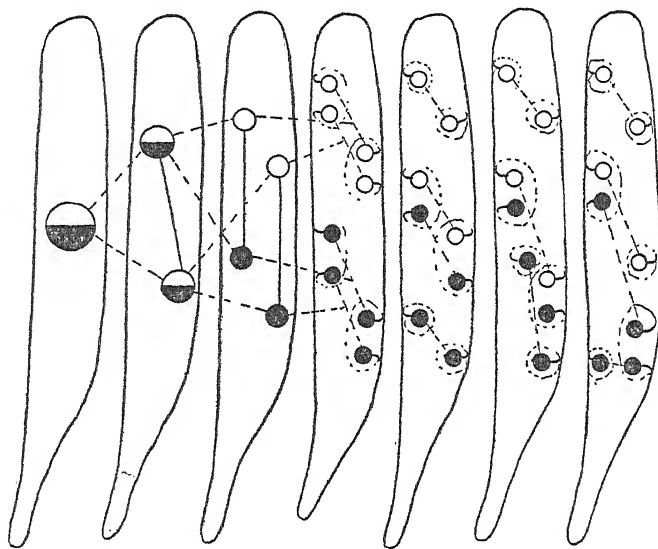
Fig. 4. Diagram showing some of the results that might be expected if segregation of sex factors occurred at the second division in the ascus, with the nuclei oriented opposite to the manner shown in figure 3, b.

portant factor in preventing two adjacent nuclei of opposite sex from forming a single bisexual spore. (Further evidence of this nature is given by asci 119, 134, and 154, in which unisexual nuclei 2 and 5 (fig. 4) apparently unite to cut out one large bisexual spore.)

All of the above described asci are easily referred to the diagrams in text figure 3, a (adapted from Dodge, 1927). These all show the result of first-division segregation of the sex factors. However, asci 119, 134, and 154 cannot be referred to this scheme. They are more easily explained as arrangements which might result from second-division segregation of the sex factors. Text figures 3, b, and 4 show two possibilities of second-division

segregation. The former is identical to that resulting from first-division segregation. The latter arrangement is equally likely to occur, if the orientation of the chromosomes in the binucleate stage in the ascus is the result of pure chance. An extended discussion can be avoided if the reader compares the asci 119, 134, and 154 with the scheme and arrangements shown in text figure 4. In spite of the fact that the sex of some of the spores was not determined, it seems clear that, in these asci, the sex factors were segregated at the second division.

In this strain of *N. tetrasperma*, there was a striking difference in the cultural characters of the mycelium produced from unisexual spores of
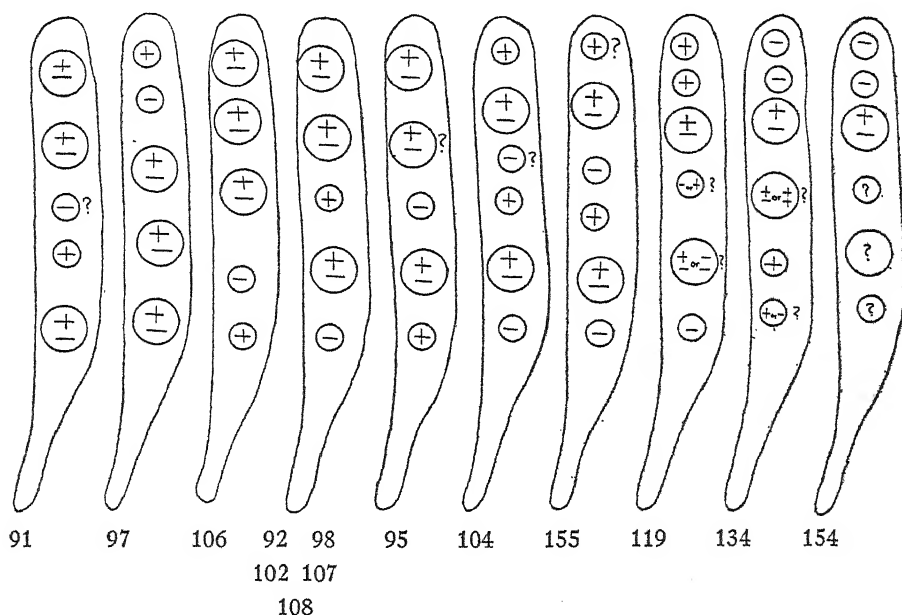
Fig. 5. Sex and arrangement of the spores in 14 abnormal asci of *N. tetrasperma*.

opposite sex. One sex produced abundant orange conidia and no color in the substrate. The other sex produced only a few white conidia and a dark, almost black, substrate.

In asci 119, 134, and 154 unisexual nuclei 1 and 2 were of the same sex and near to each other, and their beaks were probably oriented together. The fact that they did not form a single unisexual spore seems to indicate that nuclei of opposite sex cooperate in this process more readily than those of like sex. However, it is not impossible for two nuclei of like sex to form a large spore, for Dodge and the writer have both found large unisexual spores.

DISCUSSION

It has been demonstrated, in the case of *Neurospora crassa*, that the sex factors were segregated only at the first two divisions in the ascus. The ratio of first- to second-division segregation was 85 to 15. In view of this fact, it is interesting to note that both first- and second-division segregation of the sex factors occurred in *N. tetrasperma*. But first-division segregation was more frequent, as in the case of *N. crassa*. This is shown by the preponderance of asci containing four bisexual spores. It is possible, as Dodge points out, to obtain four bisexual spores by first-, second-, or third-division segregation of the sex factors. But in the case of second- or third-division segregation, the arrangement of the chromosomes would have to be determined by some means other than pure chance. In the case of second-division segregation of the sex factors of *N. crassa*, the writer has shown that there are four possibilities. Table 8 shows that, in spite of a very questionable preference for a certain orientation, all four possible orientations were found. This is an indication that, in *N. crassa*, the data do not eliminate pure chance as determining the orientation of the chromosomes on the spindle. In view of these data and the generally accepted fact that the chromosomes are oriented on the meiotic spindle by chance, as is proved in the case of *Drosophila*, it seems reasonable to assume that the orientation of the chromosomes of *N. tetrasperma* is also determined largely, if not wholly, by chance. If this is the case, the preponderance of asci with four bisexual spores means a preponderance of first-division segregation of the sex factors.

In the case of *N. sitophila*, sufficient data have not been accumulated to determine the ratio of first- to second-division segregation, or to show that this ratio is constant. But it has been shown that both first- and second-division segregations occur. It seems very likely, in view of the evidence so far obtained, that, in *N. tetrapserma* and *N. sitophila*, it will be found, on subsequent investigation, that there is a constant ratio of first- to second-division segregation of the sex factors. It will be interesting to know if this ratio is 85 to 15 as in the case of *N. crassa*.

SUMMARY

1. It has been shown that segregation of the sex factors may occur at either the first or second division in the ascus of *Neurospora crassa*.

2. Segregation of the sex factors at the third division in the ascus of *N. crassa* has not been found.

3. The ratio of first- to second-division segregation of the sex factors is 85 to 15 in *N. crassa*. This ratio is constant, in *N. crassa*, and is not determined by genic factors.

4. Both first- and second-division segregations of the sex factors have been found in the ascus of *N. tetrasperma*.

5. In the ascus of *N. tetrasperma* also, the sex factors are segregated more frequently at the first than at the second division in the ascus.

6. In *N. sitophila* segregation of the sex factors occurs at both the first and second division in the ascus.

7. A study of three generations of *N. sitophila* shows that spores from either type of ascus, on inbreeding, will produce both types of asci.

8. The data suggest the possibility that in all three species of *Neurospora* the ratio of asci in which the sex factors are segregated at the first division to those in which they are segregated at the second division is constant and cannot be modified by selection.

9. The question as to whether this ratio is the same in all three species is raised.

This work was begun at the suggestion of Professor T. H. Morgan, and it is his interest and support which have made it possible to continue the study. The writer wishes to express his thanks for criticism of the manuscript to Doctor Morgan and to Dr. B. O. Dodge, whose careful cytological work on the orientation of the spindles in the asci of the three species of *Neurospora* paved the way to interpretation of the data of this study.

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A discussion of tautonyms

Harold N. Moldenke

A rather unnecessary problem in botanical nomenclature has arisen in recent years. Although the repetition of a generic name as a specific name within that genus has always been forbidden by the international rules of nomenclature, yet a great many such combinations (known technically as tautonyms) have appeared in various botanical works during the last half century. In some cases the results of the use of these combinations have not been especially confusing, for even an amateur botanical student on seeing such combinations as *Linaria Linaria, Hystrix Hystrix, Catalpa Catalpa, Malus Malus,* and *Sassafras Sassafras* knows that *Linaria vulgaris, Hystrix patula, Catalpa bignonioides, Malus sylvestris,* and *Sassafras variifolium* are the plants which the writer has in mind. In some cases, however, where an old genus is divided to form one or more new genera (like, for example, *Polygonum* and *Persicaria*), the result is more unfortunate. One may heartily approve of the segregation of the new genus, but one may be faced with a combination in this new genus (as, for instance, *Persicaria Persicaria*) which is a violation of the rules and which one therefore does not wish to use. Often it happens that the only other name for such a plant in common use or to be found in the more popular handbooks and manuals is one in the original genus (as in the case of *Persicaria Persicaria,* the only other name for which to be found in the average handbook or manual being *Polygonum Persicaria*). The botanist, therefore, who does not have the facilities for making extensive researches into botanical literature, is faced with the alternative of either using a name in the new genus which he knows to be against the rules or not accepting the newly segregated genus at all and continuing to use the old generic name for species which he personally feels ought to be segregated. It is in the hope of being able to be of some assistance to any who may be faced with such a problem as this that the following notes have been prepared.[1]

"Double binomials" or tautonyms are more numerous in botanical literature than is commonly supposed—228 being recorded in the following list. All except six of these were published during the last fifty-two years—83 having appeared in the decade of 1880–89, 87 in the decade of 1890–99, 29 in the decade of 1900–09, 20 in the decade of 1910–19, and 9 in the decade of 1920–29. The remaining six, however, are surprising in that they date back from 58 to 163 years—one having appeared in 1873, one in 1851,

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[1] The writer wishes to express his deep appreciation and thanks to Dr. John Hendley Barnhart, who has kindly assisted in the assembling of these nomenclatural notes.

one in 1829, one in 1812, and two in 1768. The botanists responsible for these names are thirty-six in number, and their names are given in the following table as well as the number of tautonyms herein accredited to each.

Karsten..............86	Sargent...............3	Dörfler..................1
Huth...............28	Hill..................2	Griggs..................1
Britton.............26	Wettstein............2	Jirasek..................1
Voss...............18	W. F. Wight..........2	Kerner..................1
MacMillan..........9	Barnhart.............1	Keyserling.............1
Small..............9	Beauvois.............1	Kuntze.................1
Millspaugh........7	Borbás...............1	Maxon.................1
Cockerell...........6	Britton & Rose........1	Murrill........... 1
Druce..............5	Christ............ ...1	Nash........... 1
Lyons... 5	Coulter..............1	Newman....... 1
Ascherson & Graebner. 4	Degen...............1	Nieuwland... 1
Rydberg.............4		Rusby..................1

Many of the botanists, however, who are herein credited with the publication of new tautonyms published many more such duplicate combinations than are here accredited to them. This was due to their almost universal ignorance of, or at least unfamiliarity with, the works of the other men in this field, causing each to suppose that the combination which he wished to propose had never yet been published when, in reality, it had already appeared in literature often many years previous. Lyons, for instance, in his "Plant Names" published over twenty tautonyms as new, when in reality all but five had already appeared in earlier works of other botanists. MacMillan in 1892 published *Eragrostis Eragrostis*, *Nelumbo Nelumbo*, *Phragmites Phragmites*, and *Taraxacum Taraxacum* as new combinations, apparently entirely ignorant of the fact that Karsten had published all of these tautonyms in his "Deutsche Flora" in 1880–83, while Karsten, in turn, overlooked the fact that Beauvois had published the first of these as far back as 1812! A great many of the combinations in the following list are either not at all recorded in the "Index Kewensis" or its supplements, or are therein inaccurately accredited, thus greatly adding to the present confusion as to the correct authorities for certain of these names. The combination *Abies Abies*, for instance, is accredited in the "Index Kewensis" (Suppl. 7. 1929) to Druce in 1925, while in reality it was published by Rusby thirty-three years earlier. In the following list a special effort has been made to trace each name back to its original source of publication. Names like *Epipogum Epipogium*, *Atamasco Atamosco*, *Ananassa Ananas*, *Carum Carui*, *Sesbania Sesban*, *Sebesten Sebestena*, etc., which are not tautonyms in the strict interpretation of this term are not here considered.

The only other list of tautonyms which makes any pretense of being exhaustive to be found in botanical literature is that of Huth in "Helios" (11:132–136. 1893) wherein are listed 117 of these combinations. His list, however, is obsolete now because of the many new tautonyms which have been published since 1893. It is also incomplete for the period up to 1893 and contains many errors. The names given as the oldest in the segregated genera in at least 18 cases are incorrect—there being older valid ones in each case—while a number of such common combinations as *Hepatica triloba, Libanotis montana, Linaria vulgaris,* and *Rocella tinctoria* are incorrectly accredited. No specific references are made to the exact place of publication of the names cited. Still another error is the statement that the publication of tautonyms is primarily a practice of North American botanists—an opinion which is said to be widespread among European botanists even at the present time. A glance at the table given above will show that 16 of the 36 botanists there mentioned where Europeans and published 154 of the 228 tautonyms herein cited.

ABELMOSCHUS ABELMOSCHUS (L.) Karst. Fl. Deutschland, ed. 2, 2: 157. 1895.
    = *Abelmoschus moschatus* Medic. Malv. 46. 1787.
ABIES ABIES (L.) Rusby, Bull. Pharm. 6: 310. 1892.
    = *Abies excelsa* Poir. Encyc. 6: 518. 1804.
ABRUS ABRUS (L.) W. F. Wight, Contrib. U. S. Nat. Herb. 9: 171. 1905.
    = *Abrus precatorius* L. Syst., ed. 12, 472. 1767.
ABUTILON ABUTILON (L.) Huth, Helios 11: 132. 1893.
    = *Abutilon Theophrasti* Medic. Malv. 28. 1787.
ACINOS ACINOS (L.) Huth, Helios 11: 132. 1893.
    = *Acinos thymoides* Moench, Meth. 407. 1794.
ACISANTHERA ACISANTHERA (L.) Britton, Sci. Surv. P. R. & Virgin Isls. 6: 2. 1925.
    = *Acisanthera quadrata* Juss. ex Poir. in Lam. Encycl. Suppl. 1: 111. 1810.
ADHATODA ADHATODA (L.) Huth, Helios 11: 132. 1893.
    = *Adhatoda vasica* Nees in Wall. Pl. As. Rar. 3: 103. 1832.
AEGINETIA AEGINETIA (L.) Huth, Helios 11: 132. 1893.
    = *Aeginetia indica* L. Sp. Pl. 632. 1753.
ALHAGI ALHAGI (L.) Huth, Helios 11: 132. 1893.
    = *Alhagi maurorum* Medic., Vorles. Churpf. Phys. Ges. 2: 397. 1787.
ALLIARIA ALLIARIA (L.) Huth, Helios 11: 132. 1893.
    = *Alliaria officinalis* Andrz. in DC. Reg. Veg. Syst. 2: 489. 1821.
ALNUS ALNUS (L.) Britton in Britton & Br. Ill. Fl., ed. 2, 1: 613. 1913.
    = *Alnus vulgaris* Hill, Brit. Herb. 510. 1756.
AMELANCHIER AMELANCHIER (L. f.) Karst. Deutsch. Fl. 784. 1882.
    = *Amelanchier vulgaris* Moench, Meth. 682. 1794.
AMPHICARPON AMPHICARPON (Pursh) Nash, Mem. Torr. Bot. Club 5: 352. 1894.
    = *Amphicarpon Purshii* Kunth, Rev. Gram. 28. 1829.
AMSONIA AMSONIA (L.) Britton, Mem. Torr. Bot. Club 5: 262. 1894.
    = *Amsonia Tabernaemontana* Walt. Fl. Carol. 98. 1788.

ANACAMPSEROS ANACAMPSEROS (L.) Aschers. & Graebn. Syn. Mitteleur. Fl. 5^1: 429. 1915.
  = *Anacampseros Thelephiastrum* DC. Cat. Hort. Monsp. 87. 1813.
ANANAS ANANAS (L.) Voss, Vilmorin's Blumeng., ed. 3, 1: 964. 1895.
  = *Ananas sativus* Schult. f. in Roem. & Schult. Syst. 7: 1283. 1830.
ANANDRIA ANANDRIA (L.) Huth, Helios 11: 133. 1893.
  = *Anandria Bellidiastrum* DC. Prodr. 7: 40. 1839.
ANARRHINUM ANARRHINUM (L.) Druce, Rep. Bot. Exch. Cl. Brit. Isles 1924, 7: 688. 1925.
  = *Anarrhinum bellidifolium* (L.) Desf. Fl. Atlant. 2: 51. 1800.
ANDROSAEMUM ANDROSAEMUM (L.) Huth, Helios 11: 133. 1893.
  = *Androsaemum officinale* All. Fl. Pedem. 2: 147. 1785.
ANGUINA ANGUINA (L.) Huth, Helios 11: 133. 1893.
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  = *Anthriscus vulgaris* Pers. Syn. Pl. 1: 320. 1805.
APIOS APIOS (L.) MacM., Bull. Torr. Bot. Club 19: 15. 1892.
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ARCHANGELICA ARCHANGELICA (L.) Karst. Deutsch. Fl. 843. 1882.
  = *Archangelica officinalis* Hoffm. Gen. Umb. 162. 1814.
ARIA ARIA (L.) Huth, Helios 11: 133. 1893.
  = *Aria nivea* Host, Fl. Austr. 2: 8. 1831.
ARISARUM ARISARUM (L.) Huth, Helios 11: 133. 1893.
  = *Arisarum vulgare* Targ.-Tozz., Ann. Mus. Fis. Fir. 2^2: 67. 1810.
ARMENIACA ARMENIACA (L.) Huth, Helios 11: 133. 1893.
  = *Armeniaca vulgaris* Lam. Encycl. 1: 2. 1783.
ARMERIA ARMERIA (L.) Karst. Fl. Deutschland, ed. 2, 2: 489. 1895.
  = *Armeria vulgaris* Willd. Enum. Hort. Berol. 333. 1809.
ARMORACIA ARMORACIA (L.) Cockerell, Univ. Missouri Studies, Ser. 2, no. 2, 130. 1911.
  = *Armoracia rusticana* Gaertn. Meyer & Scherb. Fl. Wett. 2: 426. 1800.
ARUNCUS ARUNCUS (L.) Karst. Deutsch. Fl. 779. 1882.
  = *Aruncus silvester* Kostel. ex Maxim. in Hort. Pet. 6: 169. 1879.[2]
BALSAMINA BALSAMINA (L.) Huth, Helios 11: 133. 1893.
  = *Balsamina hortensis* Desp., Dict. Sc. Nat. 3: 485. 1816.
BALSAMITA BALSAMITA (L.) Rydb., N. Am. Fl. 34: 238. 1916.
  = *Balsamita major* Desf., Act. Soc. Hist. Nat. Paris 1: 3. 1792.
BAMBUSA BAMBUSA Huth, Helios 11: 133. 1893.
  = *Bambusa Bambos* (L.) Druce, Rep. Bot. Exch. Cl. Brit. Isles 1916, 608. 1917.
BARBAREA BARBAREA (L.) MacM. Metasp. Minn. 259. 1892.
  = *Barbarea vulgaris* R. Br. in Ait. Hort. Kew., ed. 2, 4: 109. 1812.
BATATAS BATATAS (L.) Karst. Deutsch. Fl. 973. 1882.
  = *Batatas edulis* Choisy, Conv. Or. 53. 1834.
BELLIDIASTRUM BELLIDIASTRUM (L.) Karst. Deutsch. Fl. 1066. 1883.
  = *Bellidiastrum Mitchelii* Cass., Dict. Sc. Nat. 4: 70. 1816.

  [2] This name is accredited by most authors to Kosteletzky in "Ind. Hort. Prag. 15. 1844" where it appears as a *nomen nudum*. The name was not validly published until 1879 when Maximowicz accompanied Kosteletzky's *nomen nudum* with a description and list of synonymy.

BENZOIN BENZOIN (L.) Coulter, Mem. Torr. Bot. Club 5: 164. 1894.
    = *Benzoin aestivale* (L.) Nees, Syst. Laur. 495. 1836.
BERNARDIA BERNARDIA (L.) Millsp., Field Columb. Mus. Bot. 2: 58. 1900.
    = *Bernardia carpinifolia* Griseb. Fl. Brit. W. I. 45. 1864.
BEURERIA BEURERIA (Willd.) Huth, Helios 11: 133. 1893.
    = *Beureria succulenta* Jacq. Enum. Pl. Carib. 14. 1760.
BIHAI BIHAI (L.) Griggs, Bull. Torr. Bot. Club 31: 445. 1904.
    = *Bihai borinquena* Griggs, Bull. Torr. Bot. Club 31: 445. 1904.
BLECHUM BLECHUM (L.) Millsp., Field Columb. Mus. Bot. 2: 100. 1900.
    = *Blechum pyramidatum* (Lam.) Urb. in Fedde, Repert. 15: 323. 1918.
BLEPHARIGLOTTIS BLEPHARIGLOTTIS (Willd.) Rydb. in Britton Man. 296. 1901.
    = *Blephariglottis albiflora* Raf. Fl. Tellur. 2: 38. 1836.[3]
CAJAN CAJAN (L.) Huth, Helios 11: 133. 1893.
    = *Cajanus flavus* DC. Cat. Hort. Monsp. 85. 1813.
CAKILE CAKILE (L.) Karst. Deutsch. Fl. 663. 1882.
    = *Cakile maritima* Scop. Fl. Carn., ed. 2, 2: 35. 1772.
CALAMAGROSTIS CALAMAGROSTIS (L.) Karst. Deutsch. Fl. 378. 1881.
    = *Calamagrostis lanceolata* Roth, Tent. Fl. Germ. 1: 34. 1788.
CALAMINTHA CALAMINTHA (L.) Karst. Deutsch. Fl. 1002. 1882.
    = *Calamintha officinalis* Moench, Meth. 409. 1794.
CAMPHORA CAMPHORA (L.) Karst. Deutsch. Fl. 504. 1881.
    = *Camphora officinarum* Nees, in Wall. Pl. As. Rar. 2: 72. 1831.
CANELLA CANELLA (L.) Karst. Deutsch. Fl. 626. 1882.
    = *Canella alba* Murr. Syst., ed. 14, 443. 1784.
CANTHARELLUS CANTHARELLUS (L.) Karst. Deutsch. Fl. 100. 1880.
    = *Cantharellus cibarius* Fries, Syst. Myc. 1: 318. 1821.
CARAGANA CARAGANA (L.) Karst. Deutsch. Fl. 697. 1882.
    = *Caragana arborescens* Lam. Encycl. 1: 615. 1783.
CARDUNCELLUS CARDUNCELLUS (L.) Huth, Helios 11: 133. 1893.
    = *Carduncellus monspeliensium* All. Fl. Pedem. 1: 154. 1785.
CARPINUS CARPINUS (L.) Sarg. Gard. & For. 364. 1893.
    = *Carpinus japonica* Blume, Mus. Bot. Lugd. Batav. 1: 308. 1850.
CARPOBOLUS CARPOBOLUS (L.) Karst. Deutsch. Fl. 108. 1880.
    = *Carpobolus albicans* Willd. Fl. Berol. 414. 1787.
CASTANEA CASTANEA (L.) Karst. Deutsch. Fl. 495. 1881.
    = *Castanea sativa* Mill. Gard. Dict., ed. 8, no. 1. 1768.
CATALPA CATALPA (L.) Karst. Deutsch. Fl. 927. 1882.
    = *Catalpa bignonioides* Walt. Fl. Carol. 64. 1788.
CEDRUS CEDRUS (L.) Voss, Vilmorin's Blumeng., ed. 3, 1: 1231. 1895.
    = *Cedrus Libani* Barrel. ex Loud. Arb. 2402. 1838.
CENTAURIUM CENTAURIUM (L.) W. F. Wight, Contrib. U. S. Nat. Herb. 11: 449. 1906.
    = *Centaurium umbellatum* Gilib. Fl. Lithuan. 1: 35. 1781.

[3] The *Platanthera holopetala* of Lindley (Gen. & Sp. Orch. 291. 1835), considered synonymous with this species by Rydberg (Britton & Br. Ill. Fl., ed. 2, 1: 557. 1913), seems on account of its suborbicular sepals, its linear and entire petals, and its lanceolate and less fringed lip, to be distinct, either as a variety (as maintained by Gray) or as a separate species (as originally claimed by Lindley).

CEREFOLIUM CEREFOLIUM (L.) Britton in Britton & Br. Ill. Fl., ed. 2, 2: 629. 1913.
    = *Cerefolium sativum* Bess. Prim. Fl. Galic. 1: 219. 1809.
CETARACH CETARACH (L.) Newm. Phytol. App. 5, ante p. 105. 1851.
    = *Cetarach officinarum* DC. in Lam. & DC. Fl. Franc. 2: 566. 1805.
CHAMAECRISTA CHAMAECRISTA (L.) Britton, Bull. Torr. Bot. Club 44: 12. 1917.
    = *Chamaecrista Pavonis* Cass. ex Greene, Pittonia 3: 241. 1897.[4]
CHAMOMILLA CHAMOMILLA (L.) Rydb., N. Am. Fl. 34: 231. 1916.
    = *Chamomilla patens* Gilib. Exerc. Phyt. 178. 1792.
CHLOROXYLON CHLOROXYLON (Roxb.) Huth, Helios 11: 133. 1893.
    = *Chloroxylon Swietenia* DC. Prodr. 1: 625. 1824.
CHYTRACULIA CHYTRACULIA (L.) Millsp., Field Columb. Mus. Bot. 2: 80. 1900.
    = *Chytraculia arborea* Kuntze, Rev. Gen. Pl. 238. 1891.
CIMICIFUGA CIMICIFUGA (L.) Karst. Deutsch. Fl. 571. 1882.
    = *Cimicifuga foetida* L. Syst., ed. 12, 659. 1767.
CINNAMOMUM CINNAMOMUM (L.) Karst. Deutsch. Fl. 503. 1881.
    = *Cinnamomum zeylanicum* Blume, Bijd. Fl. Ned. Ind. 568. 1825.
CITRULLUS CITRULLUS (L.) Karst. Deutsch. Fl. 889. 1882.
    = *Citrullus vulgaris* Schrad. in Eckl. & Zeyh. Enum. 279. 1836.
CLANDESTINA CLANDESTINA (L.) Huth, Helios 11: 134. 1893.
    = *Clandestina rectiflora* Lam. Fl. Fr. 2: 328. 1778.
CLINOPODIUM CLINOPODIUM (Benth.) Degen in Magyar Bot. Lap. 4: 131. 1905.
    = *Clinopodium vulgare* L. Sp. Pl. 587. 1753.
COLOCASIA COLOCASIA (L.) Huth, Helios 11: 134. 1893.
    = *Colocasia antiquorum* Schott, Meletem. 1: 18. 1832.
COLUBRINA COLUBRINA (Jacq.) Millsp., Field Columb. Mus. Bot. 2: 69. 1900.
    = *Colubrina ferruginosa* Brongn., Ann. Sc. Nat. Sér. 1, 10: 369. 1827.
CONAMI CONAMI (Sw.) Britton, Sci. Surv. P. R. & Virgin Isls. 5: 475. 1924.
    = *Conami brasiliensis* Aubl. Pl. Guian. 2: 927. 1775.
CORALLORRHIZA CORALLORRHIZA (L.) Karst. Deutsch. Fl. 448. 1881.[5]
    = *Corallorrhiza trifida* Chatelain, Spec. Inaug. 8. 1760.
CORONARIA CORONARIA (L.) Huth, Helios 11: 134. 1893.
    = *Coronaria tomentosa* A. Br., Flora 26: 368. 1843.
CORONOPUS CORONOPUS (L.) Karst. Deutsch. Fl. 673. 1882.
    = *Coronopus Ruellii* All. Fl. Pedem. 1: 256. 1785.
COTINUS COTINUS (L.) Sarg. Gard. & For. 4: 340. 1891.
    = *Cotinus coggygria* Scop. Fl. Carn., ed. 2, 1: 220. 1772.
COTONEASTER COTONEASTER (L.) Karst. Deutsch. Fl. 785. 1882.
    = *Cotoneaster integerrima* Medic. Gesch. 85. 1829.
CRUPINA CRUPINA (L.) Karst. Deutsch. Fl. 1126. 1883.
    = *Crupina vulgaris* Pers. ex Cass., Dict. Sc. Nat. 12: 68. 1818.
CUBEBA CUBEBA (L.) Karst. Deutsch. Fl. 478. 1881.
    = *Cubeba officinalis* Raf. Sylv. Tellur. 84. 1838.
CURCAS CURCAS (L.) Britton & Millsp. Bahama Fl. 225. 1920.
    = *Curcas indica* A. Rich. in Sagra, Hist. Cuba 11: 208. 1850.

[4] This name is accredited by some authors to Cassini in "Dict. Sci. Nat. 8: 78.
1817," but was never authentically published until by Greene in 1897.
[5] This combination is spelled *Coralliorrhiza Coralliorrhiza* by Aschers. & Graebn.
in Fl. Nordostd. Flachl. 220. 1898.

CYANUS CYANUS (L.) Hill, Hort. Kew. 64. 1768.
    = *Cyanus dentatofolius* Gilib. Fl. Lithuan. 1: 191. 1781.
CYDONIA CYDONIA (L.) Karst. Deutsch. Fl. 783. 1882.
    = *Cydonia oblonga* Mill. Gard. Dict., ed. 8, no. 1. 1768.
CYMBALARIA CYMBALARIA (L.) Wettst. in Engl. & Prantl, Nat. Pflanzenfam. 4: Abt.
    3b, 58. 1891.
    = *Cymbalaria muralis* Gaertn. Meyer & Scherb. Fl. Wett. 2: 397. 1800.
CYNOCRAMBE CYNOCRAMBE (L.) Huth, Helios 11: 134. 1893.
    = *Cynocrambe prostrata* Gaertn. Fruct. & Sem. 1: 362, *pl. 75*. 1788.
DALEA DALEA (L.) MacM. Metasp. Minn. 330. 1892.
    = *Dalea alopecuroides* Willd. Sp. Pl. 3: 1336. 1800.
DAMASONIUM DAMASONIUM (L.) Druce, Brit. Pl. List, ed. 2, 116. 1928.
    = *Damasonium stellatum* Thuill. Fl. Par., ed. 2, 186. 1799.
DIERVILLA DIERVILLA (L.) MacM., Bull. Torr. Bot. Club 19: 15. 1892.[6]
    = *Diervilla Lonicera* Mill. Gard. Dict., ed. 8. 1768.
DONAX DONAX (L.) Aschers. & Graebn. Fl. Nordostd. Flachl. 101. 1898.
    = *Donax arundinaceus* Beauv. Es. Agrost. *pl. 16, f. 4*. 1812.
DRACUNCULUS DRACUNCULUS (L.) Voss, Vilmorin's Blumeng., ed. 3, 1: 1166. 1895.
    = *Dracunculus vulgaris* Schott, Meletem. 1: 17. 1832.
DRYOPTERIS DRYOPTERIS (L.) Britton in Britton & Br. Ill. Fl., ed. 2, 1: 23. 1913.
    = *Dryopteris Linneana* C. Ch. Ind. Fil. 275. 1905.
ECASTOPHYLLUM ECASTOPHYLLUM (L.) Huth, Helios 11: 134. 1893.
    = *Ecastophyllum Brownei* Pers. Syn. Pl. 2: 277. 1807.
ECBOLIUM ECBOLIUM (L.) Voss, Vilmorin's Blumeng., ed. 3, 1: 812. 1895.
    = *Ecbolium Linnaeanum* S. Kurz, Journ. As. Soc. Beng. 40[2]: 75. 1871.
ECHITES ECHITES (L.) Britton ex Small, Fl. Miami 147, 200. 1913.
    = *Echites umbellata* Jacq. Enum. Pl. Carib. 13. 1760.
ENTADA ENTADA (L.) Huth, Helios 11: 134. 1893.
    = *Entada monostachya* DC. Mém. Lég. 422, *pl. 61*. 1825.
EPIPOGON EPIPOGON (Crantz) Kern. Sched. Fl. Austro-Hung. 6: 105. 1893.
    = *Epipogon aphyllum* (Schm.) Sw. Summ. Veg. Scand. 32. 1814.
ERAGROSTIS ERAGROSTIS (L.) Beauv. Es. Agrost. Pl. 10. 1812.[7]
    = *Egragrostis minor* Host, Fl. Austr. 1: 135. 1827.
ERUCA ERUCA (L.) Aschers. & Graebn. Fl. Nordostd. Flachl. 362, 1898.
    = *Eruca sativa* Mill. Gard. Dict., ed. 8, no. 1. 1768.
ERUCAGO ERUCAGO (L.) Huth, Helios 11: 134. 1893.
    = *Erucago dentata* Moench, Meth. 278. 1794.
ERUCASTRUM ERUCASTRUM (L.) Huth, Helios 11: 134. 1893.
    = *Erucastrum Pollichii* Schimp. & Spenn. in Spenn. Fl. Friburg. 3: 946. 1829.
FAGARA FAGARA (L.) Small, Fl. SE. U. S. 674, 1333. 1903.
    = *Fagara Pterota* L. Syst., ed. 10, 897. 1759.
FAGOPYRUM FAGOPYRUM (L.) Karst. Deutsch. Fl. 522. 1881.
    = *Fagopyrum esculentum* Moench, Meth. 290. 1794.
FALCARIA FALCARIA (L.) Karst. Deutsch. Fl. 835. 1882.
    = *Falcaria vulgaris* Bernh. Syst. Verz. Erf. 176. 1800.

[6] This combination is spelled *Diervillea Diervillea* by Voss in Vilmorin's Blumeng.,
ed. 3, 1: 420. 1894.
[7] Vid. A. S. Hitchcock "*Eragrostis Eragrostis* (L.) Beauv." in Erythrea 2: 37–39. 1894.

FICARIA FICARIA (L.) Karst. Deutsch. Fl. 565. 1882.
    = *Ficaria verna* Huds. Fl. Angl. 214. 1762.
FILIPENDULA FILIPENDULA (L.) Voss, Vilmorin's Blumeng., ed. 3, 1: 240. 1894.
    = *Filipendula hexapetala* Gilib. Fl. Lithuan. 2: 237. 1781.
FOENICULUM FOENICULUM (L.) Karst. Deutsch. Fl. 837. 1882.
    = *Foeniculum vulgare* Hill, Brit. Herb. 413. 1756.
FRANGULA FRANGULA (L.) Karst. Deutsch. Fl. 868. 1882.
    = *Frangula Alnus* Mill. Gard. Dict., ed. 8, no. 1. 1768.
FUMANA FUMANA (L.) Karst. Deutsch. Fl. 633. 1882.
    = *Fumana vulgaris* Spach, Ann. Sc. Nat. Sér. 2, 6: 359. 1836.
GALACTITES GALACTITES (L.) Druce, Brit. Pl. List, ed. 2, 63. 1928.
    = *Galactites tomentosa* Moench, Meth. 558. 1794.
GALEOBDOLON GALEOBDOLON (L.) Karst. Deutsch. Fl. 1010. 1883.
    = *Galeobdolon luteum* Huds. Fl. Angl., ed. 2, 1: 258. 1778.
GLAUCIUM GLAUCIUM (L.) Karst. Deutsch. Fl. 649. 1882.
    = *Glaucium flavum* Crantz, Stirp. Austr. 2: 131. 1763.
GUAZUMA GUAZUMA (L.) Cockerell, Bull. Torr. Bot. Club 19: 95. 1892.
    = *Guazuma ulmifolia* Lam. Encycl. 3: 52. 1789.
HABENARIA HABENARIA (L.) Small, Fl. SE. U. S. 316, 1329. 1903.
    = *Habenaria macroceratitis* (Sw.) Willd. Sp. Pl. 4: 44. 1805.
HELENIUM HELENIUM (Nutt.) Small, Fl. SE. U. S. 1292, 1341. 1903.
    = *Helenium leptopoda* Wood, Am. Bot. & Flor. 182. 1870.
HELIANTHEMUM HELIANTHEMUM (L.) Karst. Deutsch. Fl. 633. 1882.
    = *Helianthemum Chamaecistus* Mill. Gard. Dict., ed. 8, no. 1. 1768.
HELLEBORINE HELLEBORINE (L.) Druce, Rep. Bot. Exch. Cl. Brit. Isles 1924, 7: 689.
    1925.
    = *Helleborine latifolia* (All.) Druce, Dillen. Herb. 115. 1907.
HEPATICA HEPATICA (L.) Karst. Deutsch. Fl. 559. 1882.
    = *Hepatica triloba* Chaix in Vill. Hist. Pl. Dauph. 1: 336. 1786.
HYPOPITYS HYPOPITYS (L.) Small, Mem. Torr. Bot. Club 4: 137. 1893.
    = *Hypopitys multiflora* Scop. Fl. Carn., ed. 2, 1: 285. 1760.
HYSTRIX HYSTRIX (L.) Millsp. Fl. W. Va. 474. 1892.
    = *Hystrix patula* Moench, Meth. 295. 1794.
INGA INGA (L.) Britton, Fl. Bermuda 170. 1918.
    = *Inga vera* Willd. Sp. Pl. 4: 1010. 1806.
JAMBOS JAMBOS (L.) Lyons, Pl. Names 206. 1900.
    = *Jambosa vulgaris* DC. Prodr. 3: 286. 1828.
JUPUNBA JUPUNBA (Willd.) Britton & Rose, N. Am. Fl. 23: 27. 1928.
    = *Jupunba trapezifolia* (Vahl) Moldenke [see below].
KARATAS KARATAS (Jacq.) Voss, Vilmorin's Blumeng., ed. 3, 1: 963. 1895.
    = *Karatas Plumieri* E. Morr. Belg. Hortic. 131. 1872.
LABLAB LABLAB (L.) Lyons, Pl. Names 212. 1900.
    = *Lablab vulgaris* Savi, Diss. 19. 1821.
LABURNUM LABURNUM (L.) Dörfler, Herb. Norm. no. 3815. 1899.[8]
    = *Laburnum anagyroides* Medic., Vorles. Churpf. Phys. Ges. 2: 363. 1787.

[8] This combination appears to have been first used by Voss (as a synonym) in Vilmorin's Blumeng., ed. 3, 1: 198. 1894.

LAGENARIA LAGENARIA (L.) Cockerell, Bull. Torr. Bot. Club 19:95. 1892.
  = *Lagenaria vulgaris* Séringe, Mém. Soc. Phys. Genèv. 31: 25. 1825.
LAPPA LAPPA (L.) Karst. Deutsch. Fl. 1121. 1883.
  = *Lappa officinalis* All. Fl. Pedem. 1: 145. 1785.
LAPPULA LAPPULA (L.) Karst. Deutsch. Fl. 979. 1882.
  = *Lappula echinata* Gilib. Fl. Lithuan. 1: 25. 1781.
LARIX LARIX (L.) Karst. Deutsch. Fl. 326. 1881.
  = *Larix decidua* Mill. Gard. Dict., ed. 8, no. 1. 1768.
LENS LENS (L.) Huth, Helios 11: 134. 1893.
  = *Lens esculenta* Moench, Meth. 131. 1794.
LEONTOPODIUM LEONTOPODIUM (L.) Karst. Deutsch. Fl. 1074. 1883.
  = *Leontopodium alpinum* Cass., Dict. Sc. Nat. 25: 474. 1822.
LEPTOSTACHYS LEPTOSTACHYS (L.) MacM. Metasp. Minn. 442. 1892.
  = *Leptostachys carolinensis* Kuntze, Rev. Gen. 508. 1891.
LEUCANTHEMUM LEUCANTHEMUM (L.) Rydb., N. Am. Fl. 34: 235. 1916.
  = *Leucanthemum vulgare* Lam. Fl. Fr. 2: 137. 1778.
LEVISTICUM LEVISTICUM (L.) Karst. Deutsch. Fl. 844. 1882.
  = *Levisticum officinale* Koch, Nov. Act. Nat. Cur. 12¹: 101, *f. 41.* 1824.
LIBANOTIS LIBANOTIS (L.) Karst. Deutsch. Fl. 842. 1882.
  = *Libanotis montana* Crantz, Stirp. Austr., ed. 1, 3: 117. 1767.
LIMONIUM LIMONIUM (L.) Lyons, Pl. Names 225. 1900.
  = *Limonium vulgare* Mill. Gard. Dict., ed. 8, no. 1. 1768.
LINARIA LINARIA (L.) Karst. Deutsch. Fl. 947. 1882.
  = *Linaria vulgaris* Hill, Brit. Herb. 108. 1756.
LINOSYRIS LINOSYRIS (L.) Karst. Deutsch. Fl. 1066. 1883.
  = *Linosyris vulgaris* Cass. ex Less. Syn. Comp. 195. 1832.
LITCHI LITCHI (Lour.) Britton, Fl. Bermuda 226. 1918.
  = *Litchi chinensis* Sonner. Voy. Ind. 2: 230. 1782.
LUFFA LUFFA (L.) Lyons, Pl. Names 231. 1900.
  = *Luffa aegyptiaca* Mill. Gard. Dict., ed. 8. 1768.
LYCOPERSICUM LYCOPERSICUM (L.) Karst. Deutsch. Fl. 966. 1882.[9]
  = *Lycopersicum esculentum* Mill. Gard. Dict., ed. 8. 1768.
MAJORANA MAJORANA (L.) Karst. Deutsch. Fl. 999. 1882.
  = *Majorana hortensis* Moench, Meth. 406. 1794.
MALUS MALUS (L.) Britton in Britton & Br. Ill. Fl., ed. 2, 2: 290. 1913.[10]
  = *Malus sylvestris* Mill. Gard. Dict., ed. 8, no. 1. 1768.
MALVAVISCUS MALVAVISCUS (L.) Voss, Vilmorin's Blumeng., ed. 3, 1: 142. 1894.
  = *Malvaviscus arboreus* Cav. Diss. 3: 131, *pl. 48, f. 1.* 1790.
MANIHOT MANIHOT (L.) Karst. Deutsch. Fl. 588. 1882.
  = *Manihot utilissima* Pohl, Fl. Bras. Ic. 1: 32, *pl. 24.* 1827.
MARIANA MARIANA (L.) Hill, Hort. Kew. 61. 1768.
  = *Mariana lactea* Hill, Herb. Brit. 1: 75. 1769.
MARISCUS MARISCUS (L.) Borbás, Balaton Fl. 321. 1900.
  = *Mariscus serratus* Gilib. Exerc. Phyt. 2: 512. 1792.

[9] This combination is spelled *Lycopersicon Lycopersicon* by Britton in Britton & Br. Ill. Fl., ed. 2, 3: 168. 1913.
[10] This combination appears to have been first used by Voss (as a synonym) in Vilmorin's Blumeng., ed. 3, 1: 275. 1894.

MELOCACTUS MELOCACTUS (L.) Karst. Deutsch. Fl. 888. 1882.
     =*Melocactus communis* Link & Otto, Verh. Preuss. Ver. Gartenb. 3: 417, *pl. 11.*
     1827.
METHYSTICUM METHYSTICUM (Forst.) Lyons, Pl. Names 247. 1900.
     =*Methysticum esculentum* Raf. Sylv. Tellur. 85. 1838.
METOPIUM METOPIUM (L.) Small, Fl. SE. U. S. 726, 1334. 1903.
     =*Metopium Linnaei* Engl. in DC. Monog. Phan. 4: 367. 1883.
MEUM MEUM (L.) Karst. Deutsch. Fl. 839. 1882.
     =*Meum athamanticum* Jacq. Fl. Austr. 4: 2. 1776.
MOLDAVICA MOLDAVICA (L.) Britton in Britton & Br. Ill. Fl., ed. 2, 3: 115. 1913.
     =*Moldavica suaveolens* Gilib. Fl. Lithuan. 1: 79. 1781.
MONNIERA MONNIERA (L.) Britton, Mem. Torr. Bot. Club 5: 292. 1894.
     =*Monniera Brownei* Pers. Syn. Pl. 2: 166. 1806.
MORINGA MORINGA (L.) Millsp., Field Mus. Bot. 1: 490. 1902.
     =*Moringa oleifera* Lam. Encycl. 1: 398. 1783.
MUSCARI MUSCARI (L.) Voss, Vilmorin's Blumeng., ed. 3, 1: 124. 1894.
     =*Muscari moschatum* Willd. Enum. Hort. Berol. 378. 1809.
NASTURTIUM NASTURTIUM (L.) Cockerell, Bull. Torr. Bot. Club 19: 95. 1892.
     =*Nasturtium officinale* R. Br. in Ait. Hort. Kew., ed. 2, 4: 111. 1812.
NEGUNDO NEGUNDO (L.) Karst. Deutsch. Fl. 596. 1882.
     =*Negundo aceroides* Moench, Meth. 334. 1794.
NELUMBO NELUMBO (L.) Karst. Deutsch. Fl. 553. 1882.
     =*Nelumbo nucifera* Gaertn. Fruct. & Sem. 1: 73, *pl. 19.* 1788.
NUMMULARIA NUMMULARIA (Bull.) Karst. Deutsch. Fl. 138. 1881.
     =*Nummularia Bulliardi* Tul. Sel. Fungor. Carp. 2: 43, *pl. 5, f. 11–19.* 1863.
NYCTELEA NYCTELEA (L.) Britton in Britton & Br. Ill. Fl., ed. 2, 3: 67. 1913.
     =*Nyctelea americana* Moldenke [see below].
NYMPHOIDES NYMPHOIDES (L.) Druce, Brit. Pl. List, ed. 2, 79. 1928.
     =*Nymphoides orbiculata* Gilib. Fl. Lithuan. 1: 33. 1781.
ODONTITES ODONTITES (L.) Wettst. in Engl. & Prantl, Nat. Pflanzenfam. 4: Abt. 3b,
     102. 1891.
     =*Odontites rubra* Gilib. Fl. Lithuan. 1: 126. 1781.
OMPHALODES OMPHALODES (L.) Voss, Vilmorin's Blumeng., ed. 3, 1: 693. 1895.
     =*Omphalodes verna* Moench, Meth. 420. 1794.
ONOBRYCHIS ONOBRYCHIS (L.) Karst. Deutsch. Fl. 681. 1882.
     =*Onobrychis viciaefolia* Scop. Fl. Carn., ed. 2, 2: 76. 1772.
OPOPANAX OPOPANAX (L.) Karst. Deutsch. Fl. 847. 1882.
     =*Opopanax Chironium* Koch, Nov. Act. Nat. Cur. 12[1]: 96. 1825.
OPUNTIA OPUNTIA (L.) Karst. Deutsch. Fl. 888. 1882.
     =*Opuntia compressa* (Salisb.) Macbr., Contrib. Gray Herb. 65: 41. 1922.
ORNUS ORNUS (L.) Karst. Deutsch. Fl. 1045. 1883.
     =*Ornus europaea* Pers. Syn. Pl. 1: 8. 1805.
OSTRYA OSTRYA (L.) MacM. Metasp. Minn. 187. 1892.
     =*Ostrya virginiana* (Mill.) Willd. Sp. Pl. 4: 469. 1805.
OSTRYA OSTRYA (L.) Sarg. Silv. N. Am. 9: 32. 1896.
     =*Ostrya carpinifolia* Scop. Fl. Carn., ed. 2, 2: 244. 1772.
OTOBA OTOBA (Humb. & Bonpl.) Karst. Deutsch. Fl. 578. 1882.
     =*Otoba novogranatensis* Moldenke [see below].

OXYCOCCUS OXYCOCCUS (L.) MacM., Bull. Torr. Bot. Club 19: 15. 1892.
    =*Oxycoccus palustris* Pers. Syn. Pl. 1: 419. 1805.
PALIURUS PALIURUS (L.) Karst. Deutsch. Fl. 870. 1882.
    =*Paliurus australis* Gaertn. Fruct. & Sem. 1: 203, *pl. 43.* 1788.
PAPAYA PAPAYA (L.) Karst. Deutsch. Fl. 894. 1882.
    =*Papaya communis* Noronha, Verh. Batav. Gen. 5, ed. 1, art. 4, 23. 1790.
PARSONSIA PARSONSIA (L.) Britton ex Northrop, Mem. Torr. Bot. Club 12: 53. 1902.
    =*Parsonsia herbacea* J. St. Hil. Exp. Fam. Nat. 2: 173. 1805.
PAVIA PAVIA (L.) Huth, Helios 11: 135. 1893.
    =*Pavia octandra* Mill. Gard. Dict., ed. 8, no. 1. 1768.
PENTSTEMON PENTSTEMON (L.) Britton, Mem. Torr. Bot. Club 5: 291. 1894.[11]
    =*Pentstemon laevigatus* Soland. in Ait. Hort. Kew. 2: 300. 1789.
PENTSTEMON PENTSTEMON (L.) MacM., Bull. Torr. Bot. Club 19: 15. 1892.
    =*Pentstemon hirsutus* (L.) Willd. Sp. Pl. 3: 227. 1801.
PERESKIA PERESKIA (L.) Karst. Deutsch. Fl. 888. 1882.[12]
    =*Pereskia aculeata* Mill. Gard. Dict., ed. 8. 1768.
PERSEA PERSEA (L.) Cockerell, Bull. Torr. Bot. Club 19: 95. 1892.
    =*Persea gratissima* Gaertn. f. Fruct. & Sem. 3: 222. 1807.
PERSICARIA PERSICARIA (L.) Small, Fl. SE. U. S. 378, 1330. 1903.
    =*Persicaria mitis* Gilib. Exerc. Phyt. 431. 1792.
PETASITES PETASITES (L.) Karst. Deutsch. Fl. 1062. 1883.
    =*Petasites officinalis* Moench, Meth. 568. 1794.
PETROSELINUM PETROSELINUM (L.) Karst. Deutsch. Fl. 831. 1882.
    =*Petroselinum sativum* Hoffm. Gen. Umb. 177. 1814.
PHEGOPTERIS PHEGOPTERIS (L.) Keyserling, Polyp. & Cyath. Herb. Bung. 50. 1873.
    =*Phegopteris polypodioides* Fée, Gen. Fil. 243. 1852.
PHRAGMITES PHRAGMITES (L.) Karst. Deutsch. Fl. 379. 1881.
    =*Phragmites communis* Trin. Fund. Agrost. 134. 1820.
PHYMATODES PHYMATODES (L.) Maxon, Contrib. U. S. Nat. Herb. 9: 352. 1905.
    =*Phymatodes vulgaris* Presl, Tent. 196. 1836.
PHYSALODES PHYSALODES (L.) Britton, Mem. Torr. Bot. Club 5: 287. 1892.[13]
    =*Physalodes peruvianum* Kuntze, Rev. Gen. 452. 1891.
PIMENTA PIMENTA (L.) Karst. Deutsch. Fl. 790. 1882.
    =*Pimenta officinalis* Lindl. Coll. Bot. sub *pl. 19.* 1821.
POLYGONATUM POLYGONATUM (L.) Voss, Vilmorin's Blumeng., ed. 3, 1: 1069. 1895.[14]
    =*Polygonatum officinale* All. Fl. Pedem. 1: 131. 1785.
POLYPORUS POLYPORUS (Retz) Murrill, Bull. Torr. Bot. Club 31: 33. 1904.
    =*Polyporus brumalis* (Pers.) Fries, Obs. Myc. 2: 255. 1818.
POROPHYLLUM POROPHYLLUM (L.) Kuntze, Rev. Gen. Pl. 3²: 168. 1898.
    =*Porophyllum ellipticum* Cass., Dict. Sc. Nat. 43: 56. 1826.

[11] This combination is spelled *Pentastemon Pentastemon* by Voss in Vilmorin's Blumeng., ed. 3, 1: 768. 1895.
[12] This combination is spelled *Piereskia Piereskia* by Voss in Vilmorin's Blumeng., ed. 3, 1: 385. 1894.
[13] This combination is erroneously spelled *Physaloides Physaloides* by Durand & Jackson in Ind. Kew. Suppl. 1: 328. 1903.
[14] This combination appears (as a synonym) accredited to Jirasek in Roemer & Schultes Syst. Veg. 7: 299. 1829.

PULEGIUM PULEGIUM (L.) Karst. Deutsch. Fl. 997. 1882.
    =*Pulegium vulgare* Mill. Gard. Dict., ed. 8, no. 1. 1768.
PULICARIA PULICARIA (L.) Karst. Deutsch. Fl. 1072. 1883.
    =*Pulicaria vulgaris* Gaertn. Fruct. & Sem. 2: 461, *pl. 173*. 1791.
PULSATILLA PULSATILLA (L.) Karst. Deutsch. Fl. 560. 1882.
    =*Pulsatilla vulgaris* Mill. Gard. Dict., ed. 8, no. 1. 1768.
PYRACANTHA PYRACANTHA (L.) Voss, Vilmorin's Blumeng., ed. 3, 1: 269. 1894.
    =*Pyracantha coccinea* M. Roem. Syn. fasc. 3, Rosifl., 219. 1847.
QUAMOCLIT QUAMOCLIT (L.) Britton in Britton & Br. Ill. Fl., ed. 1, 3: 22. 1898.
    =*Quamoclit vulgaris* Choisy in DC. Prodr. 9: 336. 1845.
RADIOLA RADIOLA (L.) Karst. Deutsch. Fl. 606. 1882.
    =*Radiola linoides* Roth, Tent. Fl. Germ. 1: 71. 1788.
RAPHANISTRUM RAPHANISTRUM (L.) Karst. Deutsch. Fl. 673. 1882.
    =*Raphanistrum Lampsana* Gaertn. Fruct. & Sem. 2: 300, *pl. 143*. 1791.
RHAPONTICUM RHAPONTICUM (L.) Voss, Vilmorin's Blumeng., ed. 3, 1: 554. 1894.
    =*Rhaponticum scariosum* Lam. Fl. Fr. 2: 38. 1778.
RICINELLA RICINELLA (L.) Britton ex P. Wilson, Bull. N. Y. Bot. Gard. 8: 395. 1917.
    =*Ricinella pedunculosa* Muell. Arg., Linnaea 34: 153. 1865.
ROCELLA ROCELLA (L.) Karst. Deutsch. Fl. 164. 1881.
    =*Rocella tinctoria* DC. Fl. Fr. 2: 334. 1805.
SANGUISORBA SANGUISORBA (L.) Britton, Mem. Torr. Bot. Club 5: 189. 1894.
    =*Sanguisorba minor* Scop. Fl. Carn., ed. 2, 1: 110. 1772.
SASSAFRAS SASSAFRAS (L.) Karst. Deutsch. Fl. 505. 1881.
    =*Sassafras variifolium* (Salisb.) Kuntze, Rev. Gen. Pl. 574. 1891.
SCOLOPENDRIUM SCOLOPENDRIUM (L.) Karst. Deutsch. Fl. 278. 1881.
    =*Scolopendrium vulgare* Symons, Mém. Ac. Turin 5: 421, *pl. 9, f. 2*. 1793.
SCOPOLIA SCOPOLIA (L.) Karst. Deutsch. Fl. 962. 1882.
    =*Scopolia carniolica* Jacq. Obs. Bot. 1: 32, *pl. 20*. 1764.
SCORODONIA SCORODONIA (L.) Karst. Deutsch. Fl. 1016. 1883.
    =*Scorodonia heteromalla* Moench, Meth. 384. 1794.
SELLIGUEA SELLIGUEA (Mett.) Christ, Bull. Boiss. 6²: 992. 1906.
    =*Selliguea membranacea* Blume, Enum. Pl. addend. 1828.
SESBAN SESBAN (L.) Britton, Mem. Brooklyn Bot. Gard. 1: 54. 1918.
    =*Sesbania aegyptica* Pers. Syn. Pl. 2: 316. 1807.
SILAUS SILAUS (L.) Karst. Deutsch. Fl. 836. 1882.
    =*Silaus flavescens* Bernh. Syst. Verz. Erf. 174. 1800.
SOJA SOJA (L.) Karst. Deutsch. Fl. 711. 1882.
    =*Soja Max* (L.) Piper, U. S. Dept. Agr. Bur. Pl. Ind. Invent. Seeds & Pl. Import. 33: 53. 1915.
SOPHIA SOPHIA (L.) Britton in Britton & Br. Ill. Fl., ed. 1, 2: 144. 1897.
    =*Sophia multifida* Gilib. Exerc. Phyt. 1: 243. 1792.
SORGHUM SORGHUM (L.) Karst. Deutsch. Fl. 367. 1881.
    =*Sorghum vulgare* Pers. Syn. Pl. 1: 101. 1805.
STROBUS STROBUS (L.) Small, Fl. SE. U. S. 29, 1326. 1903.
    =*Strobus Weymouthiana* Opiz, Lotos 4: 94. 1854.
SUCCISA SUCCISA (L.) Karst. Deutsch. Fl. 1053. 1883.
    =*Succisa pratensis* Moench, Meth. 489. 1794.

SYMPHORICARPOS SYMPHORICARPOS (L.) MacM., Bull. Torr. Bot. Club 19: 15. 1892.[15]
  = *Symphoricarpos orbiculatus* Moench, Meth. 503. 1794.
TARAXACUM TARAXACUM (L.) Karst. Deutsch. Fl. 1138. 1883.
  = *Taraxacum officinale* Weber, Prim. Pl. Holst. 56. 1780.
THELYPTERIS THELYPTERIS (L.) Nieuwland, Midland Nat. 1: 226. 1910.
  = *Thelypteris palustris* Schott, Gen. *pl. 10.* 1834.
THEVETIA THEVETIA (L.) Karst. Deutsch. Fl. 1035. 1883.
  = *Thevetia nereifolia* Juss. ex Steud. Nom. Bot., ed. 2, 2: 680. 1841.
TOXICODENDRON TOXICODENDRON (L.) Britton in Britton & Br. Ill. Fl., ed. 2, 2: 484.
  1913.
  = *Toxicodendron pubescens* Mill. Gard. Dict., ed. 8, no. 2. 1768.
TUBER TUBER (L.) Karst. Deutsch. Fl. 131. 1881.
  = *Tuber cibarium* Sibth. Flor. Oxon. 398. 1794.
UGNI UGNI (Mol.) Voss, Vilmorin's Blumeng., ed. 3, 1: 315. 1894.
  = *Ugni Molinae* (Barn.) Turcz., Bull. Soc. Nat. Mosc. 21¹: 579. 1848.
ULMARIA ULMARIA (L.) Barnh., Bull. Torr. Bot. Club 21: 491. 1894.
  = *Ulmaria palustris* Moench, Meth. 663. 1794.
UVA-URSI UVA-URSI (L.) Cockerell ex Daniels, Univ. Missouri Studies Sc. Ser. 2, no. 2,
  186. 1911.
  = *Uva-ursi procumbens* Moench, Meth. 470. 1794.
VACCARIA VACCARIA (L.) Britton in Britton & Br. Ill. Fl., ed. 1, 2: 18. 1897.
  = *Vaccaria vulgaris* Host, Fl. Austr. 1: 518. 1827.
VANILLA VANILLA (L.) Karst. Deutsch. Fl., ed. 2, 1: 474. 1895.
  = *Vanilla planifolia* Andr. Bot. Rep. 8: *pl. 538.* 1808.
VINCETOXICUM VINCETOXICUM (L.) Karst. Deutsch. Fl. 1030. 1883.
  = *Vincetoxicum officinale* Moench, Meth. 717. 1794.
VIORNA VIORNA (L.) Small, Fl. SE. U. S. 439, 1331. 1903.
  = *Viorna urnigera* Spach, Hist. Veg. Phan. 7: 270. 1839.
VISCARIA VISCARIA (L.) Voss ex Aschers. & Graebn. Fl. Nordostd. Flachl. 299. 1898.[16]
  = *Viscaria vulgaris* Roehl. Deutsch. Fl., ed. 2, 2: 275. 1812.
VITICELLA VITICELLA (L.) Small, Fl. SE. U. S. 437, 1330. 1903.
  = *Viticella deltoidea* Moench, Meth. 297. 1794.
VITIS-IDAEA VITIS-IDAEA (L.) Britton, Bull. N. Y. Bot. Gard. 3: 179. 1903.
  = *Vitis-Idaea punctata* Moench, Meth. 47. 1794.
ZINGIBER ZINGIBER (L.) Karst. Deutsch. Fl. 471. 1881.
  = *Zingiber officinale* Roscoe, Trans. Linn. Soc. 8: 348. 1807.
ZIZYPHUS ZIZYPHUS (L.) Karst. Deutsch. Fl. 870. 1882.
  = *Zizyphus sativa* Gaertn. Fruct. & Sem. 1: 202. 1788.

In this connection it is interesting to note the number of important synonyms which are omitted from the majority of our popular manuals and handbooks—even in many cases from works which as a rule give

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[15] This combination is spelled *Symphoricarpus Symphoricarpus* by Huth in Helios 11: 136. 1893.

[16] This combination appears to have been first used (as a synonym) by Voss in Vilmorin's Blumeng., ed. 3, 1: 100. 1894.

rather complete lists of synonymy for other species. Many of these synonyms are important because of their relation to the shifting of species from one genus to another and to the process of splitting up of old genera into smaller ones which seems to be the practice in so many quarters of the botanical world today. Many of the larger and more generally accepted genera are being divided into smaller segregates by present day monographers, and many others have been so divided in the past. It happens, however, that many of the names thus produced have been overlooked in popular lists of synonymy and one is frequently confronted with problems such as the following: Britton & Brown's Illustrated Flora maintains the genus *Padus* as distinct from the genus *Prunus*, while Gray's New Manual of Botany does not. Now, if the fifteen or more species of racemose cherries are to be kept distinct, as the genus *Padus*, from the ninety-five or more umbellate and corymbose species (the genus *Prunus* proper), then it is obvious that the *Prunus Padus* of Linnaeus, mentioned in Gray's School and Field Book of Botany, belongs to the genus *Padus* and not *Prunus*. And yet a botanist unable to avail himself of the research facilities of a large botanical library finds himself unable to label any specimens of *Prunus Padus* which he may happen to collect because nowhere in any popular work on American wild or cultivated plants, is there any synonym given for *Prunus Padus* within the genus *Padus*. He cannot use the combination *Padus Padus* because of the international rules of nomenclature which explicitly forbid such a repetition. He must, therefore, either accept the name *Padus* for all other species of racemose cherries except that one and still continue to call the European Bird Cherry a "Prunus," or else not adopt the name *Padus* at all and continue to call all cherries, both the racemose and the corymbose, by the name "Prunus."

In the following list a few of the more interesting of these cases are presented. In some instances (as, for example, in the case of *Amygdalus*, *Padus*, *Sorbus*, *Grossularia*, *Melilotus*, etc.) the segregated genera are today accepted as valid genera by numerous taxonomists of recognized standing. The opportunity presented in these instances for the manufacture of new tautonyms has so far, fortunately, been overlooked. The labors of the tautonym-makers, thus, while extensive, have by no means exhausted the opportunities for making such combinations. It is to be sincerely hoped, however, in view of the continued disfavor with which such bizarre combinations are regarded by the great majority of botanists throughout the world and at all international botanical congresses, that no more such "double binomials" will appear in the future and necessitate any supplement to the list given on the preceding pages.

ACORUS CALAMUS L. Sp. Pl. 324. 1753.
  Calamus aromaticus Gueldenst. in Ledeb. Fl. Ross. 4: 13. 1853.
AESCULUS HIPPOCASTANUM L. Sp. Pl. 344. 1753.
  Hippocastanum vulgare Gaertn. Fruct. & Sem. 2: 135, *pl. 3*. 1791.
ALLIUM CEPA L. Sp. Pl. 300. 1753.
  Cepa prolifera Moench, Meth. 244. 1794.
ARBUTUS UNEDO L. Sp. Pl. 395. 1753.
  Unedo edulis Hoffmgg. & Link, Fl. Port. 1: 415. 1809.
ARTEMISIA ABSINTHIUM L. Sp. Pl. 848. 1753.
  Absinthium vulgare Lam. Fl. Fr. 2: 45. 1778.
CROTON TIGLIUM L. Sp. Pl. 1004. 1753.
  Tiglium officinale Klotzsch, Nov. Act. Nat. Cur. 19, suppl. 1, 418. 1843.
CUCURBITA PEPO L. Sp. Pl. 1010. 1753.
  Pepo vulgaris Moench, Meth. 653. 1794.
CYPERUS PAPYRUS L. Sp. Pl. 47. 1753.
  Papyrus antiquorum Willd., Abh. Acad. Berl. 70. 1812.
DATURA STRAMONIUM L. Sp. Pl. 179. 1753.
  Stramonium foetidum Scop. Fl. Carn., ed. 2, 1: 157. 1772.
DAUCUS CAROTA L. Sp. Pl. 242. 1753.
  Carota sativa Rupr. Fl. Ingric. 468. 1860.
GARCINIA MANGOSTANA L. Sp. Pl. 443. 1753.
  Mangostana Garcinia Gaertn. Fruct. & Sem. 2: 105. 1791.
HIPPOMANE MANCINELLA L. Sp. Pl. 1191. 1753.
  Mancinella venenata Tussac, Fl. Antill. 3: 21, *pl. 5*. 1824.
HUMULUS LUPULUS L. Sp. Pl. 1028. 1753.
  Lupulus Humulus Mill. Gard. Dict., ed. 8. 1768.
ILEX AQUIFOLIUM L. Sp. Pl. 125. 1753.
  Aquifolium Ilex Scop. Fl. Carn., ed. 2, 1: 116. 1772.
IMPERATORIA OSTRUTHIUM L. Sp. Pl. 259. 1753.
  Ostruthium officinale Link, Handb. 1: 360. 1829.
JUNIPERUS SABINA L. Sp. Pl. 1039. 1753.
  Sabina officinalis Garcke, Fl. Deutschl., ed. 4, 387. 1849.
LEONURUS CARDIACA L. Sp. Pl. 584. 1753.
  Cardiaca vulgaris Moench, Meth. 401. 1794.
LONICERA CAPRIFOLIUM L. Sp. Pl. 173. 1753.
  Caprifolium hortense Lam. Fl. Fr. 3: 365. 1792.
LONICERA PERICLYMENUM L. Sp. Pl. 173. 1753.
  Periclymenum vulgare Mill. Gard. Dict., ed. 8, no. 6. 1768.
LONICERA XYLOSTEUM L. Sp. Pl. 174. 1753.
  Xylosteon dumetorum Moench, Meth. 502. 1794.
LYSIMACHIA NUMMULARIA L. Sp. Pl. 148. 1753.
  Nummularia repens Gilib. Fl. Lithuan. 1: 29. 1781.
LYTHRUM SALICARIA L. Sp. Pl. 446. 1753.
  Salicaria vulgaris Moench, Meth. 665. 1794.
MATTEUCCIA STRUTHEOPTERIS (L.) Todaro, Syn. Pl. Acot. Vasc. Silicia 30. 1866.
  Strutheopteris filicastrum All. Fl. Pedem. 2: 283. 1785.
MELIA AZADIRACHTA L. Sp. Pl. 385. 1753.
  Azadirachta indica A. Juss., Mém. Mus. Par. 19: 220. 1830.

MELIA AZEDARACH L. Sp. Pl. 384. 1753.
 Azedarach Commelini Medic. Bot. Beobacht. 164. 1782.
MIRABILIS JALAPA L. Sp. Pl. 177. 1753.
 Jalapa officinalis Crantz, Inst. **2**: 266. 1766.
NARCISSUS JONQUILLA L. Sp. Pl. 290. 1753.
 Jonquilla major Haw. Monog. Narciss. 7. 1831.
NEPETA CATARIA L. Sp. Pl. 570. 1753.
 Cataria tomentosa Gilib. Fl. Lithuan. **1**: 78. 1781.
NEPETA GLECHOMA Benth. Lab. Gen. & Sp. 485. 1834.
 Glecoma hederacea L. Sp. Pl. 578. 1753.
NERIUM OLEANDER L. Sp. Pl. 209. 1753.
 Oleander vulgaris Medic., Act. Acad. Theod. Palat. 6, phys. 381. 1790.
NICOTIANA TABACUM L. Sp. Pl. 180. 1753.
 Tabacum ovatofolium Gilib. Fl. Lithuan. **1**: 39. 1781.
OENANTHE PHELLANDRIUM Lam. Fl. Fr. **3**: 432. 1778.
 Phellandrium aquaticum L. Sp. Pl. 255. 1753.
PHACELIA WHITLAVIA A. Gray, Proc. Am. Acad. **10**: 321. 1875.
 Whitlavia grandiflora Harv. in Hook. Lond. Journ. Bot. **5**: 312. 1846.
PHYLLANTHUS EMBLICA L. Sp. Pl. 982. 1753.
 Emblica officinalis Gaertn. Fruct. & Sem. **2**: 122, *pl. 108, f. 2.* 1791.
PHYSALIS ALKEKENGI L. Sp. Pl. 183. 1753.
 Alkekengi officinarum Moench, Meth. Suppl. 177. 1802.
PIMPINELLA ANISUM L. Sp. Pl. 264. 1753.
 Anisum vulgare Gaertn. Fruct. & Sem. **1**: 23. 1788.
POTENTILLA TORMENTILLA Neck., Act. Acad. Theod. Palat. **2**: 491. 1770.
 Tormentilla erecta L. Sp. Pl. 500. 1753.
PRUNUS AMYGDALUS Stokes, Bot. Mat. Med. **3**: 101. 1812.
 Amygdalus communis L. Sp. Pl. 473. 1753.
PRUNUS CERASUS L. Sp. Pl. 474. 1753.
 Cerasus vulgaris Mill. Gard. Dict., ed. 8, no. 1. 1768.
PRUNUS PADUS L. Sp. Pl. 473. 1753.
 Padus Avium Mill. Gard. Dict., ed. 8, no. 1. 1768.[17]
PSIDIUM GUAJAVA L. Sp. Pl. 470. 1753.
 Guajava pyriformis Gaertn. Fruct. & Sem. **1**: 185, *pl. 38.* 1788.
PUNICA GRANATUM L. Sp. Pl. 472. 1753.
 Granatum punicum St. Lag., Ann. Soc. Bot. Lyon, **7**: 132. 1880.
PYRUS SORBUS Gaertn. Fruct. & Sem. **2**: 45, *pl. 87.* 1791.
 Sorbus domestica L. Sp. Pl. 477. 1753.
RHAMNUS ALATERNUS L. Sp. Pl. 193. 1753.
 Alaternus Phylica Mill. Gard. Dict., ed. 8, no. 1. 1768.
RIBES GROSSULARIA L. Sp. Pl. 201. 1753.
 Grossularia reclinata (L.) Mill. Gard. Dict., ed. 8, no. 4. 1768.
ROBINIA PSEUDACACIA L. Sp. Pl. 722. 1753.
 Pseudo-Acacia vulgaris Medic., Vorles. Churpf. Phys. Ges. **2**: 364. 1787.

[17] This is not to be confused with the *Prunus Avium* of Linnaeus (Fl. Suec., ed. 2, 474. 1755), which is the common Sweet Cherry and a true member of the genus *Prunus* proper.

Rumex Acetosa L. Sp. Pl. 337. 1753.
  Acetosa magna Gilib. Exerc. Phyt. **2**: 445. 1792.
Rumex Acetosella L. Sp. Pl. 338. 1753.
  Acetosella vulgaris Fourr., Ann. Soc. Linn. Lyon, N. S. **17**: 145. 1869.
Salsola Kali L. Sp. Pl. 222. 1753.
  Kali Soda Moench, Meth. 331. 1794.
Selinum Creoselinum Crantz, Stirp. Austr., ed. 1, **3**: 33. 1767.
  Creoselinum legitimum Bieb. Fl. Taur. Cauc. **3**: 211. 1819.
Semecarpus Anacardium L. f. Suppl. 182. 1781.
  Anacardium officinarum Gaertn. Fruct. & Sem. **1**: 92. 1788.
Senecio Cineraria DC. Prodr. **6**: 355. 1837.
  Cineraria maritima L. Sp. Pl., ed. 2, 1244. 1763.
Sequoia Wellingtonia Seem., Bonplandia **3**: 27. 1855.
  Wellingtonia gigantea Lindl. Gard. Chron. 819, 823. 1853.
Solanum Dulcamara L. Sp. Pl. 185. 1753.
  Dulcamara flexuosa Moench, Meth. 514. 1794.
Theobroma Cacao L. Sp. Pl. 782. 1753.
  Cacao sativa Aubl. Pl. Guian. **2**: 689. 1775.
Trifolium Melilotus L. Sp. Pl. 764. 1753.
  Melilotus indica (L.) All. Fl. Pedem. **1**: 308. 1785.
Trigonella Foenum-Graecum L. Sp. Pl. 777. 1753.
  Foenum-Graecum sativum Medic., Vorles. Churpf. Phys. Ges. **2**: 383. 1787.
Valeriana Locusta L. Sp. Pl. 33. 1753.
  Locusta communis Delarb. Fl. Auv., ed. 2, 88. 1800.
Verbascum Blattaria L. Sp. Pl. 178. 1753.
  Blattaria vulgaris Fourr., Ann. Soc. Linn. Lyon, N. S. **17**: 125. 1869.
Verbascum Lychnitis L. Sp. Pl. 177. 1753.
  Lychnitis alba Fourr., Ann. Soc. Linn. Lyon, N. S. **17**: 125. 1869.
Verbascum Thapsus L. Sp. Pl. 177. 1753.
  Thapsus Schraderi Opiz, Seznam 96. 1852.

Jupunba trapezifolia (Vahl) Moldenke, comb. nov.

Since the generic name *Jupunba* proposed by Britton & Rose (N. Am. Fl. **23**: 24. 1928) is considered distinct from *Pithecellobium, Acacia, Inga,* and *Mimosa,* the *Acacia Jupunba* of Willdenow (Sp. Pl. **4**: 1067. 1806) must receive a new specific name. The combination *Jupunba Jupunba* proposed by Britton & Rose (N. Am. Fl. **23**: 27. 1928) is untenable because of being a tautonym. The next earliest name applied to this species, we find, is the *Mimosa trapezifolia* of Vahl (Eclog. **3**: 36. 1807). The combination *Jupunba trapezifolia* is therefore hereby proposed for this plant.

Nyctelea americana Moldenke, nom. nov.

The generic name *Nyctelea* of Scopoli (Introd. 183. 1777) was resurrected by Britton in 1913 and maintained in preference to the *Macrocalyx* of Trew (Nov. Act. Nat. Cur. **2**: 330–332. 1761) and the *Ellisia* of Lin-

naeus (Sp. Pl., ed. 2, 1662. 1763) because of the following considerations:
(1) the generic name *Macrocalyx* being a mere hyponym and (2) the generic
name *Ellisia* as published by Linnaeus in the second edition of his Species
Plantarum (1763) being a homonym of the genus of the same name pub-
lished by him in the tenth edition of his Systema Naturae (p. 1121. 1759).
Since the genus *Nyctelea*, then, is to be maintained it appears that the *Ellisia
Nyctelea* of Linnaeus (Sp. Pl., ed. 2, 1662. 1763) must take on a new specific
name. The combination *Nyctelea Nyctelea* proposed by Britton (Britton
& Br. Ill. Fl., ed. 2, 3: 67. 1913) is untenable because of Article 55 of the
Vienna Rules, the principle of which was confirmed at Cambridge in 1930.
Inasmuch as no other specific name besides that of Linnaeus appears ever
to have been applied to this plant, the name *Nyctelea americana* is hereby
proposed. Since 1913, then, four species have been placed in the genus
Nyctelea. These are as follows: (1) *Nyctelea micrantha* (Torr.) Woot. &
Standl. [Contrib. U. S. Nat. Herb. **19**: 535. 1915]; (2) *Nyctelea ambigua*
(Nutt.) Standl. [Proc. Biol. Soc. Wash. **32**: 143. 1919]; (3) *Nyctelea pine-
torum* (Jones) Tidestrom [Contrib. U. S. Nat. Herb. **25**: 442. 1925]; and
(4) *Nyctelea americana* Moldenke (*Ellisia Nyctelea* L.).

Otoba novogranatensis Moldenke, nom. nov.

Karsten in his Deutsche Flora (p. 578. 1882) appears to have been the
first to make use of the generic name *Otoba* which he there accredits to
Alphonse de Candolle. According to Karsten the genus *Otoba* is distin-
guished from *Myristica* in that the anthers stand terminal on the apex
of the filaments in the former, while in the latter they are adnate to the
filaments by their back. Since the genus *Otoba* is thus to be retained as dis-
tinct from *Myristica*, then the *Myristica Otoba* of Humboldt & Bonpland
(Pl. Aequin. **2**: 78, *pl. 103*. 1809) must be given a new specific name. The
combination *Otoba Otoba* proposed by Karsten (Deutsch. Fl. 578. 1882) is
untenable because of being a tautonym and no other specific name appears
ever to have been applied to the plant in question. The name *Otoba novo-
granatensis* is therefore hereby proposed for this plant. The only two known
species of the genus, then, are as follows: (1) *Otoba incolor* (Warb.) Karst.
(Nov. Act. Acad. Nat. Cur. **68**: 232. 1897) and (2) *Otoba novogranatensis*
Moldenke (the *Myristica Otoba* of Humboldt & Bonpland).

INDEX TO AMERICAN BOTANICAL LITERATURE

1928-1932

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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Descriptions of new species of Tertiary cycads, with a review of those previously recorded.[1]

ARTHUR HOLLICK

(WITH PLATES 1–14)

At the time when this paper was originally prepared for publication I received a copy of a similar one on the same general subject, from the author, Dr. Richard Kräusel of Frankfurt am Main.[2] The similarity between my contribution and the one by Doctor Kräusel, both in subject matter and in the manner of its presentation, may be regarded as a coincidence sufficiently interesting to be noted. I am pleased to hereby acknowledge my indebtedness to Doctor Kräusel for tracings, citations and other items of information in connection with certain Old World species, which otherwise would not have been in my possession.

DESCRIPTIONS OF NEW SPECIES
Genus CERATOZAMIA Brongniart

Ceratozamia Wrightii n. sp. (Plate 1). Leaf simply pinnate, dimensions not known. Leaflets entire, opposite or sub-opposite, normally subtending angles of about 80° with the rachis, linear-lanceolate to linear-elliptical, about 7.5 cm. in length by 1.2 cm. in maximum width, broadest below the middle, tapering distad to acute apices, more or less narrowed proximad to bases that terminate in triangular alate expansions through which they are attached to the sides of the rachis. Venation uniform, simple, parallel, the veins approximately 1 mm. or less apart.

Locality: Hamilton Bay, Kupreanof Island, Alexander Archipelago, Alaska.
Latitude: N. 57°.
Age and formation: Tertiary (Eocene) shaly sandstone.
Collector: C. W. Wright, U. S. Geological Survey, 1904.
Specimen in U. S. National Museum.

This species is, apparently, referable to the genus *Ceratozamia*, as far as may be inferred from the most striking of the surficial foliar characters that are discernible; and in order to facilitate comparison I have introduced (plate 2) a figure of a median portion of a leaf of the existing Mexican species *Ceratozamia mexicana* Brongniart, reduced to about one half

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[1] Published with the permission of the Director of the United States Geological Survey.

[2] Paläobotanische Notizen IX. Über eine Cycadee aus dem Cerithienkalken von Nierstein und über die tertiäre Verbreitung der Cycadeen. Senckenbergiana 10: 103–111. *pl. 1.* 1928.

the natural size. The blunt apices of the leaflets might be regarded as more suggestive of the genus *Zamia;* but the relatively broad bases of the leaflets and the manner of their attachment to the rachis, are characteristic of *Ceratozamia* rather than of *Zamia.*

Our specimen is the first fossil representative of the genus thus far recorded from the New World; but a Tertiary (Miocene) species (*Ceratozamia Hofmanni*) from Switzerland, represented by a single parallel-veined leaflet, was described and figured by Ettingshausen; and a somewhat similar but more fragmentary specimen, from the Tertiary (Oligocene) of Italy, was described and figured by Meschinelli under the name *Ceratozamites vicetinus.* The relationship of each of these species to the Cycadaceae has, however, been questioned. The two species are listed and discussed on page 180 in this paper.

In our existing flora the northern limit of the range of the genus *Ceratozamia* is about latitude 25°, in Mexico, its only known region of distribution; but the discovery of our fossil species, in rocks of Tertiary age in Alaska, at about latitude 57°, represents presumptive evidence that tropical or sub-tropical climatic conditions prevailed there at that time. We may also regard it as significant that, as far as any records show, this Tertiary species was confined to the western American or Pacific region, as are the existing species of the genus, indicating that, even as far back as the early part of that period, milder climatic conditions prevailed in southeastern Alaska than in equivalent latitudes in the interior and in the eastern part of the continent.

The specific name is given in honor of Mr. C. W. Wright, by whom the specimen above described was collected.

Genus Dioön Lindley

Dioön inopinus n. sp. (Plate 3). Leaf pinnate. Leaflets linear-lanceolate or ligulate, slightly falcate, attached to the sides of the rachis, entire (sparingly denticulate above the middle?), 12.5 cm. or more, in length by 1.5 cm. in width near the middle, slightly contracted and then abruptly expanded at the bases, distinct and separate from each other throughout. Venation uniform, simple, parallel, the veins approximately .5 mm. apart.

Locality: South side, near the head of Hamilton Bay, Kupreanof Island, Alexander Archipelago, Alaska.

Latitude: N. 57°.

Age and formation: Tertiary (Eocene) shale.

Collector: W. W. Atwood, U. S. Geological Survey, 1907.

Specimen in U. S. National Museum.

This specimen, although fragmentary, indicates that the leaf, in its entirety, was apparently comparable in size with the average of the exist-

ing species of the genus. The leaflets, as far as discernible, are entire; but a single, well defined denticle, on the upper margin of the second lower leaflet on the left hand side of the specimen, may indicate that the distal parts of at least some of the leaflets were denticulate.

This species, and the one next described, are the first fossil representatives of the genus *Dioön* thus far recorded from any American locality, although several species have been described under the genus *Dioönites*, in particular from Mesozoic strata, among which it may be pertinent to refer to *Dioönites borealis* Dawson,[3] from the Cretaceous of the Northwest Territory, as a near ancestral relative of the two species of *Dioön* now under consideration, from the nearby coastal region of Alaska.

It is of interest to note, as was discussed in connection with the genus *Ceratozamia*, that the last representatives of the genus *Dioön* to survive in the northern part of North America were, apparently, confined to the Pacific coast region. At least no specimens that could be referred to the genus have been found anywhere in the interior or in the eastern part of the Continent. Until as recently as early Tertiary time, and perhaps later, their northern range extended to latitude 57° in Alaska, and possibly farther, whereas the present northern limit of distribution of the genus is about latitude 30° in Mexico, where it reaches, also, its furthest eastern distribution. These facts constitute important indices of the probable climatic conditions that prevailed in the region during the early part of the Tertiary period.

On the piece of matrix that contains our specimen may be seen numerous remains of *Sequoia Langsdorfii* (Brongniart) Heer, and fragments of a leaf that appear to represent a *Fagus*.

Dioön praespinulosum n. sp. (Plate 4, figs. 1, 2). Leaves simply pinnate or sub-pinnatifid. Leaflets ligulate, tapering distad, crowded, alternately arranged, as far as discernible, attached to the sides of the rachis by the entire extent of their bases, sparingly spinose-denticulate distad, 2–6 cm. or more in length by 5–8 mm. in maximum width. Venation uniform, simple, parallel, the veins approximately .5 mm. apart.

Locality: South side, near the head of Hamilton Bay, Kupreanof Island, Alexander Archipelago, Alaska.

Latitude: N. 57°.

Age and formation: Tertiary (Eocene) shale.

Collector: W. W. Atwood, U. S. Geological Survey, 1907.

Specimen in U. S. National Museum.

[3] DAWSON, J. W. On the Cretaceous and Tertiary floras of British Columbia and the North-West Territory. Trans. Roy. Soc. Canada 1[4] [1882]: 24. *pl. 3, f. 37.* 1883.

This species is closely similar, in its general surficial appearance, to the existing Mexican species *Dioön spinulosum* Dyer, of which species a figure of a specimen (plate 5) is introduced for comparison. The general resemblance between them is unmistakable, and the minor characters may be seen to be strikingly alike.

The specimens figured on plate 4 show an upper part of a leaf (fig. 1) and a lower, median part (fig. 2). Other specimens, more or less dismembered and fragmentary, could have been selected to further illustrate the species; but the two figured should be sufficient for identification.

CYCAD (gen. et sp.?)

Locality: Kern River region, near Bakersfield, Kern County, California.
Latitude: N. 35° 25'
Geological horizon: Lower Miocene (Temblor beds).

The remains included in the above record are represented by apical parts of stumps or trunks, contained in and mostly replaced by a fine grained calcareous sandstone with numerous foraminifera, described as a marine deposit.

The specimens belong in the collection of the California Academy of Sciences. They were recently made known to me and were transmitted to me for examination through the courtesy of Dr. G. D. Hanna, Curator of the Department of Paleontology of the Academy. A cursory examination was sufficient to determine their relationship with the Cycadales; but their closer identification, if possible, was recognized as highly desirable, and I transmitted the specimens to Dr. G. R. Wieland, at Yale University, to whom I am indebted for their more critical examination. A complete report, I am advised, will be published elsewhere. Doctor Wieland stated that sections of the trunks failed to reveal plant structure of any kind. Their identity as cycadaceous remains, however, was confirmed, and relegation to the form-genus *Bucklandia* was suggested, with a specific name indicative of the locality or geologic formation. This would be in accord with the publication of *B. niersteinensis* Kräusel (see page 179) from the Miocene of Germany, and would be non-committal in regard to identity with any existing genus, or any fossil genus based upon foliar organs. Generic identity with certain of the Eocene cycads of Alaska and the existing cycads of Mexico may, however, be regarded as probable.

The locality where the specimens were found is indicated in its proper place on the map (plate 14). This locality record is of special interest as it represents a heretofore unknown but not unexpected fact in connection with the former distribution of the order.

PREVIOUSLY RECORDED SPECIES
New World—Northern Hemisphere
Genus Zamia Linnaeus

Zamia tennesseeana Berry, U. S. Geol. Survey, Prof. Paper 156: 51.
pl. 32. f. 8. 1930. (Plate 13, Fig. 4)

> *Locality:* West of Bolivar, Hardeman County, Tennessee.
> *Latitude:* N. 35° 15'
> *Geological horizon:* Lower Eocene (Wilcox group).

The author discusses the possible relationship of the species with the
Cretaceous podocarpaceous genus *Nageiopsis,* but concludes that 'the
probability is all in the direction of the present specimen representing a
cycad pinnule'.

Figure 4, plate 13 is reproduced from a tracing of Berry's figure of the
species, the description and illustration of which was published after our
plates and figures had been arranged and numbered; hence it's inclusion,
apparently out of place, with figures of Old World species, on plate 13.

As far as may be judged from an examination of the figure, the species
appears to be, surficially, almost identical with small leaflets of the existing
Zamia angustifolia Jacquin.

Zamia mississippiensis Berry, Torreya 16: 177. *f. 1–3.* 1916; U. S.
Geol. Survey, Prof. Paper 108: 63. *f. 17a, b, c.* 1917. (Plate 6, fig. 1 (a, b, c,))

> *Locality:* Meridian, Lauderdale County, Mississippi.
> *Latitude:* N. 32° 21'.
> *Geological horizon:* Lower Eocene (Wilcox group).

This species was discussed by the author (*loc. cit.*) as suggestive of the
existing *Zamia floridana* De Candolle.

Zamia (?) wilcoxensis Berry, U. S. Geol. Survey, Prof. Paper 91: 169.
pl. 114, f. 2. 1916. (Plate 6, fig. 6)

> *Locality:* Four and a half miles southeast of Naborton, De Soto Parish, Louisiana.
> *Latitude:* N. 32° 3'.
> *Geological horizon:* Lower Eocene (Wilcox group).

This species was compared by the author (*loc. cit.*) with the existing
Zamia pumila Linnaeus.

Zamia collazoënsis Hollick, Sci. Surv. Porto Rico and Virgin Islands
7[3]: 184. *pl. 53, f. 1, 3, 5, (7?).* 1928. (Plate 7, figs. 5, 6)

> *Locality:* Collazo River, base of first falls below the Lares-San Sebastian Road
> bridge, Porto Rico.
> *Latitude:* N. 18°.
> *Geological horizon:* Upper Eocene or Oligocene.

Comparable with the existing *Zamia integrifolia* Jacquin, and *Z. sali-cina* Britton.

ZAMIA NOBLEI Hollick, Sci. Surv. Porto Rico and Virgin Islands 7[3]: 185. *pl. 53, f. 9, 10; pl. 54, f. 1, 3a; pl. 55, f. 1–3, 4a, 5a.* 1928. (Plate 6, figs. 3, 4)

Locality: Collazo River, base of first falls below the Lares-San Sebastian Road bridge, Porto Rico.
Latitude: N. 18°.
Geological horizon: Upper Eocene or Oligocene.

Comparable with the existing *Zamia pumila* Linnaeus, *Z. umbrosa* Small, and *Z. integrifolia* Jacquin.

ZAMIA species, Berry, Proc. U. S. Natl. Mus. 75[24]: 2. *pl. 1, f. 6.* 1929. (Plate 6, fig. 5)

Zamites species, *idem,* p. 12.

Locality: Montserrate, near Bogota, Colombia.
Latitude: N. 5°.
Geological horizon: Oligocene?

Figure 5 (=figure 6, Berry, *loc. cit.*) is depicted in a vertical position. The original figure is in a horizontal position, with the rounded end toward the right.

This species is represented by a ligulate fragment of a parallel-veined leaflet or pinnule which is abruptly contracted or rounded to a blunt termination at the one end that is preserved intact; but whether this is the proximal or the distal end can not be satisfactorily determined, although the latter is strongly suggested by the figure. The author, however (*loc. cit.*), described the specimen as 'contracted toward the base'. The author did not offer any suggestion in regard to comparison with or similarity to any existing species; but it may be seen to be very similar, in general appearance, to the distal parts of certain of the leaflets included under *Zamia Noblei*, as may be seen by comparison with our figures 3 and 4 on plate 6. Also it might be regarded as representing the distal extremity of a leaflet of which the proximal extremity was closely similar to the specimen represented by *Zamia wilcoxensis*, as may be seen by comparison with figure 6 on plate 6. In any event all three species, as far as may be judged by the figures, are suggestively similar in general appearance.

New World—Southern Hemisphere

Genus ZAMIA Linnaeus

ZAMIA PRAECEDENS Ettingshausen in Krasser, Sitzber. K. Akad. Wiss. Wien Math.-Naturw. Cl. 112[1]: 853. 1903. [*Nom. nud.*]

Locality: Ouricanga (= Ouricanguinhas), about 25.5 km. northwest of the town of Alagoinhas, 14.7 km. north of Aramarý railroad station, Province of Bahia, Brazil.
Latitude: S. 12°.
Geological horizon: Late Tertiary (Pliocene?).

This species was not described or figured, and I have not seen the specimen. The author compared it with the existing *Zamia boliviana* De Candolle.

ZAMIA TERTIARIA Engelhardt, Abh. Senckenb. Naturforsch. Gesellsch. 16: 646. *pl. 2, f. 16.* 1891; Berry, E. W. Johns Hopkins Univ. Stud. Geol. 4: 120. *pl. 1* [misprinted 'VIII' in text], *f. 4; pl. 2,* [*f. 1–3,* not numbered on plate]. 1922. (Plate 7, figs. 1, [2, 3, 4?])

Locality: Coronel, Chile [Lota, Chile, *fide* Berry, *loc. cit.* p. 121], figs. 1, 4. Coranila-hue, Chile, figs. 2, 3.
Latitude: S. 37°.
Geological horizon: Lower (?) Miocene.

Under the above specific name Berry (*loc. cit.*) includes large leaf forms (see our plate 7, figures 2, 3) very different, in size and shape, from *Zamia tertiaria* as described and figured by Engelhardt. He also relegates to the same species a parallel veined leaf which Engelhardt (*loc. cit.,* p. 686, pl. 1, fig. 4), somewhat doubtfully, designated 'Monokotyler Blattrest'. (see our plate 7, figure 4). Apparently there could be no serious objection to regarding Engelhardt's problematical monocotyledon as specifically identical with the *Zamia* leaflets figured by Berry; but their reference to *Z. tertiaria* as described and figured by Engelhardt (*loc. cit.*) appears to be open to question—judging by comparison between the figures. Under the circumstances the following quotation from Berry's discussion of the species (*loc. cit.,* p. 121) may be of interest:

It is rather singular that with the small amount of material at his disposal Engelhardt should have recognized as representing a *Zamia* the small fragment figured by him and should have failed to recognize the relationship of the larger specimen which he refers to and figures as a fragment of a monocotyledonous leaf. This will account for the fact that Engelhardt compared the species with the existing *Zamia integrifolia* Ait. of Florida and the Antilles, when it actually is much more similar to several existing South American species.

It may also be of interest, in this connection, to compare Engelhardt's figure of *Z. tertiaria* (see our figure 1, plate 7) with *Z. collazoënsis* Hollick (fig. 5, plate 7), which latter was compared by me (Sci. Surv. Porto Rico 7³: 184) with *Z. integrifolia* Jacquin; from which it might be inferred that the species last named (not *Z. integrifolia* Aiton) is the one that Engelhardt (*loc. cit.,* p. 620) intended to designate as resembling *Z. tertiaria,* in as much as the leaflets of *Z. integrifolia* Jacquin are relatively broad and

frequently short, whereas those of *Z. integrifolia* Aiton are relatively narrow and long. It may also be pertinent to note that in each of Engelhardt's figures the proximal and distal extremities are lacking, hence satisfactory comparison with them is impossible.

ZAMIA AUSTRALIS Berry, Proc. U. S. Natl. Mus. 73[22]: 11. *pl. 2, f. 1.* 1928. (Plate 6, fig. 2)

Locality: Rio Nirihuao, near Casa Piedra, about 12 miles south of Lago Nahuel Huapi, Territory of Rio Negro, Argentina.
Latitude: S. 41°.
Geological horizon: Oligocene or lower Miocene.

The author did not compare this species with any now in existence. The fossil species which it resembles most closely—and the resemblance is remarkable— is *Zamites arcticus* Goeppert,[4] from the Lower Cretaceous (Komé) beds of Greenland.

Old World—Northern Hemisphere

Genus ZAMIPHYLLUM Caspary & Klebs

ZAMIPHYLLUM SAMBIENSE (Caspary) Caspary & Klebs, Abh. K. Preuss. Geol. Landesanst. n.s. 4: 63 (text); *pl. 8, f. 51–51a* (atlas). 1907. (Plate 8, fig. 2)

Zamites sambiensis Caspary, Schrift. K. Physik.-Ökon. Gesell. Königsberg **22**: Sitzb. p. 26. 1882.

Locality: Samland, Baltic Prussia, Germany.
Latitude: N. 54° 50′.
Geological horizon: Middle Miocene (Tortonian?).

This genus and species is based upon two overlapping fragmentary leaflet remains, included in impure amber ('Braunharz' or 'Beckerit'), 13.5 mm. in length by 7 mm. in width, described (*loc. cit*, p. 26. 1882) as having 'etwa 35 parallelen dichten Nerven, die nach unten konvergiren, gegen die Spitze ganz parallel laufen und am Rande mit kleinem Bogen nach oben endigen'. The figure that serves to illustrate the species is enlarged to five times the natural size.

ZAMITES? PALAEOCENICUS Saporta & Marion, Mém. Cour. et Mém. Sav. Etrang. Acad. Roy. Sci. Belg. **41**[3]: 20. *pl. 1, f. 4, 5.* 1878. (Plate 8, fig. 3[4,5])

Zamites eocenicus Saporta & Marion. *op. cit.* p. 10 (*nom. nud.*).
Locality: Gelinden, Belgium.
Latitude: N. 50° 45′.
Geological horizon: Paleocene (Thanatian?).

[4] GOEPPERT, H. R. N. Jahrb. Mineral. Geol. u. Paläontol. 1866: 134. *pl. 2, f. 9, 10.* 1866. HEER, OSWALD. Flora fossilis arctica. **1**: 82. *pl. 3, f. 14, 14b; pl. 44, f. 5c.* 1868.

This species is based upon two parallel-veined leaf fragments whose relationship with the Cycadaceae may, possibly, be regarded as open to question. As far as indicated by the figures the species might equally well be referred to the Monocotyledonae or, possibly, to a coniferous genus comparable with the existing *Dammara* (=*Agathis*) or *Podocarpus*; and in order to facilitate such comparison, I have introduced the accompanying text figures 1a, b, reproduced, respectively, from nature prints of leaves of *Dammara obtusa* Lindley and *Aga-gathis philippinensis Warburg*. Incidentally it may be of interest to compare all of the figures with those of *Zamia tertiaria* Engelhardt *fide* Berry. (See this paper. p. 175, pl. 7, figs. 2, 3.)

ZAMITES (DIOÖN?) TERTIARIUS HERR, Flora Tertiaria Helvetiae 1: 46. *pl. 16, f. 1* (*a, b, c, d, e*). 1855. (Plate 8, fig. 1)

Locality: Estavé, Vaud, Switzerland.
Latitude: N. 46° 30′.
Geological horizon: Miocene(Helvetian?).

This species is based upon what may be seen to be a poorly depicted specimen which, apparently, represents a fragmentary piece of a cycad leaf. The author discusses its probable relationship at some length, and finally concludes: 'Es gehört daher die fossile art wahrscheinlich zur Gattung Dion [Dioön]'. Schimper[5] suggested that 'c'est probablement un Dioön, voisin de notre *D. edule*'; and Kräusel[6] somewhat noncommittally remarked: 'Fiederbau und Nervatur sind mehr cycadeen- denn palmenähnlich'.

It would, obviously, be of little interest or value to here express any opinion in regard to the probable
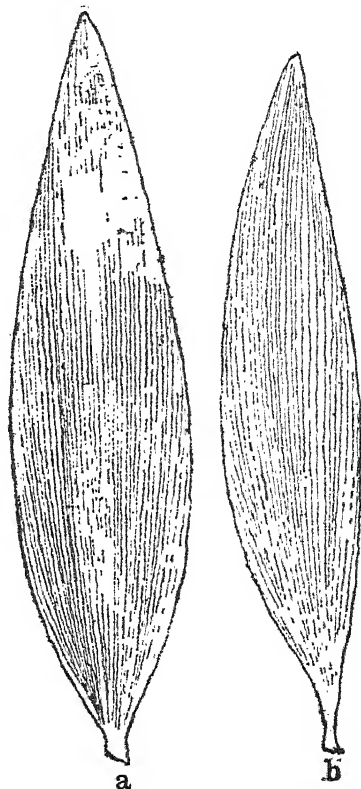
Fig. 1. a. *Dammara obtusa* Lindley. Specimen in conservatory, New York Botanical Garden. b. *Agathis philippinensis* Warburg. Luzon, March 25, 1904, *R. S. Williams 755;* specimen in herb. New York Botanical Garden.

[5] SCHIMPER, W. P. Traité de Paléontologie Végétale 2: 157. 1870.
[6] KRÄUSEL, RICHARD. Senckenbergiana 10: 106. 1928.

generic relationship of the species, in the absence of any personal examination of the specimen upon which the species was based.

ZAMITES EPIBIUS Saporta, Bull. Soc. Géol. France II. 21: 322. *pl. 5, f. 1–3.* 1864 (=*Z. ephibius* in legend on plate 5); Ann. Sci. Nat. Bot. V. 8: 10. *pl. 1, f. 1, 2.* 1867. (Plate 13, fig. 2[1,2,3])

> *Locality:* Bonnieux, Vaucluse (Provence), France.
> *Latitude:* N. 43° 45′.
> *Geological horizon:* Miocene (Aquitanian?).

Saporta's first description and illustration of this species (*loc. cit.*, 1864) included the leaf and two enlargements, reproduced in our plate 13, figure 2[1,2,3]; and his second (*loc. cit.*, 1867) included the leaf previously figured and a cone of more or less problematic botanical relationship. He (*loc. cit.*, pp. 10–11. 1867) compared the leaf with the Jurassic species *Zamia Feneonis* Brongniart[7] and *Z. formosus* Heer,[8] and the cone with female cones of the existing genus *Macrozamia*. In connection with these remains Kräusel[9] briefly comments that 'Das Blatt gehört einer Cycadee an; der damit vereinigte Zapfen ist aber wohl nur ein schlecht erhaltener, verdrückter Koniferenzapfen'.

As far as the surficial characters of the leaf and leaflets are concerned they might be regarded as indicative of relationship with *Encephalartus* rather than with *Zamia* (see *E. Gorceixianus*, plate 11).

ZAMITES RACZKIEVICZI Stur, Math. Termész. Köslem. Budapest 11: 86. 1873. [nom. nud.]

> *Locality:* Hungary?
> *Latitude:* N. 46?
> *Geological horizon:* Late Tertiary (Neogene)?

The above represents all of the information that I have been able to obtain in relation to this species. It was named, but apparently has been neither described nor figured.

Genus ZAMIOSTROBUS Endlicher

ZAMIOSTROBUS SAPORTANUS Schimper, Traité Paléont. Végétale 2: 204. *pl. 72, f. 12.* 1870.

> *Locality:* Armissan, Aude, France.
> *Latitude:* N. 43°.
> *Geological horizon:* Miocene (Aquitanian?).

[7] BRONGNIART, ADOLPHE. Dict. Sci. Nat. 57: 99 (94). 1928 [*nom. nud.*]. *Zamites Feneonis* (Brongniart) Unger. Chloris Protogaea, pt. 6, p. lxiii. 1845. Ettingshausen. Abh. K. K. Geol. Reichsanst. 1[3]: 9. *pl. 3, f. 1.* 1852.

[8] HEER, OSWALD. Urwelt der Schweiz, p. 144, *f. 94.* 1865.

[9] KRÄUSEL, RICHARD. Senckenbergiana 10: 105. 1928.

This species was based upon a cycad strobile (female?), which was originally erroneously coupled by Schimper (*op. cit.*, p. 157) with the fossil leaf remains described and figured by Saporta under the name *Zamites epibius*,[10] but was subsequently determined not to belong with the remains representing that species, and was relegated to the form genus *Zamiostrobus*. Schimper's correction of the error (*op. cit.*, p. 204) is as follows:

C'est par erreur que j'ai dit, a l'occasion du *Zamites epibius*, que M. de Saporta rapporte le cône d'Armissan à cette feuille de Zamiée, rencontré à Orbagneux avec l'empreinte d'un cône mal conservé, dont la forme et la dimensions différent beaucoup du fruit dont il est question ici; ce dernier constitue évidement une espèce particulière que rapelle assez les cônes de certaines espèces de *Zamia* de l'époque actuelle.

Genus BUCKLANDIA Presl

BUCKLANDIA NIERSTEINENSIS Kräusel, Senckenbergiana 10: 107. *pl. 1, f. 1–3.* 1928.

Locality: Nierstein, Rhenish Hessen, Germany.
Latitude: N. 49° 45'.
Geological horizon: Miocene (Aquitanian?).

This species is based upon what appear to be well defined remains of cycadaceous trunks, which the author (*loc. cit.*, p. 108) refers to the form-genus *Bucklandia*, with the suggestion that, taking all circumstances and conditions into consideration, they might, tentatively, be referred to the existing African genus *Encephalartus*.

Genus CYCADITES Sternberg

CYCADITES ESCHERI Heer, Mitth. Naturf. Gesell. Zurich, 3: 109. 1853 [*Nom. nud.*]; Flora Tertiaria Helvetiae 1: 46. *pl. 15, f. 1, 2.* 1855.

Locality: Steinerweg ob Stein, Schaffhausen, Switzerland.
Latitude: 47° 45'.
Geological horizon: Miocene (Tortonian?).

This species is based upon remains of trunks that, as far as may be judged from the figures, simulate, more or less closely, those of a cycad. The author (*loc. cit.*) remarks upon their resemblance to *Endogenites echinatus* Brongniart,[11] but says:

Der Endogenites echinatus wird nicht mit Unrecht als Palmenstamm gedeutet, während der von Stein nicht von einer Palme herrühren kann, dagegen grosse Aehnlichkeit mit dem Stamme der Cycadeen hat.

I am not aware that any authority has ventured to refer the remains to any existing genus, and the opinion has been expressed that their defi-

[10] See this paper, p. 178, Pl. 13, fig. 2.
[11] BRONGNIART, A. T. Mém. Mus. d'Hist. Nat. [Paris] 8: 301. *pl. 16* (5), *f. 2.* 1822.

nite reference to the cycads is open to question. Any opinion based only upon examination and comparison of the several figures above cited would be of little value.

Genus CERATOZAMIA Brongniart

CERATOZAMIA HOFMANNI Ettingshausen, Sitzber. K. Akad. Wiss. Wien Math.-Naturw. Cl. 96^1: 80–81. 1887; Denkschr. K. Akad. Wiss. Wien Math.-Naturw. Cl. 54: 272 [12]. *pl. 3, f. 10, (10a, 10b).* 1888. (plate 13, fig. 1)

Locality: Leoben, Styria, Austria.
Latitude: N. 47° 30'.
Geological horizon: Miocene (Mayencian?).

This species is represented by a single falcate-lanceolate leaflet, which is more or less suggestive of *Zamia tertiaria* Engelhardt *fide* Berry,[12] as far as the shape is concerned (see our plate 7, figure 3). Comparison of other characters depicted in the figures would, however, be of little value. Study of the actual specimens would be necessary in order to arrive at satisfactory conclusions in regard to any further resemblances or any differences. It may be pertinent to suggest, however, that comparison with certain of the Monocotyledonae might not be out of place.

Genus CERATOZAMITES Meschinelli

CERATOZAMITES VICETINUS Meschinelli,[13] Atti Soc. Veneto-Trentina Sci. Nat. 10: 276 [9], *pl. 6, figs. 1, 2.* 1889. (Plate 9, 10)

Locality: Monte Piano, Venetia, Italy.
Latitude: N. 45° 30'.
Geological horizon: Oligocene (Stampian?).

The author compared this species with the existing *Ceratozamia mexicana* Brongniart; but whether or not the comparison may be considered as justified will probably remain a matter of individual opinion. As far as is shown in the figures the general shape of the leaflets and their attachment to the rachis might, about equally well, be regarded as suggestive of relationship with the African genus *Encephalartus*, which reference would seem to be more logical, in view of the present geographical distribution of the two genera; but the rachis, it may be noted, is indicated as smooth and rounded, and is not strikingly suggestive of the upper or inner surface

[12] BERRY, E. W. Johns Hopkins Univ. Stud. Geol. 4: 120: *pl. 1, f. 4; pl. 2, f. 1–3.* 1922.

[13] Note. Writers subsequent to the date of Meschinelli's description of the species have written the specific name *"vicentinus,"* which would seem to be the correct rendition. A.H.

of the rachis of a cycad leaf with attached leaflets; and in this connection it may be pertinent to cite Kräusel[14], who remarked, in his discussion of the apparent affinities of the species, that it 'könnte sehr wohl auch einer Palme angehören'.

Genus ENCEPHALARTUS Lehmann
Plate 11

ENCEPHALARTUS GORCEIXIANUS Saporta, Comp. Rend. Acad. Sci. Paris **78**: 1320. 1874; La Nature **5²**: 262. *f. 9.* 1877; Soc. Bot. et Hort. Provence Bull. **2**: 42 (2). *pl.* [not numbered]. 1880.

Zamites Gorceixianus (Saporta) Renault, Cours de botanique fossile **1**: 166 (tableau), *pl. 5, f. 1.* 1880.

> *Locality:* Koumi, Island of Eubosa, Greece.
> *Latitude:* N. 38° 20'.
> *Geological horizon:* Miocene (Aquitanian?).

As far as I am aware no one has seriously questioned the validity of the reference of this species to the genus *Encephalartus*. Saporta (*loc. cit.*, pp. 43(3)–44 (4)) compared it with the existing *E. Altensteinii* Lehmann and an undescribed species from the northern interior of Africa, and remarked: 'Cette Cycadée fossile est d'autant plus intéressante qu'elle est la première qu'il ait été possible jusqu'ici d'inscrire sans anomalie dans un des genres vivants'.

Renault (*op. cit.*, p. 53) listed the species under Saporta's binomial, but included it, with other fossil species, under the genus *Zamites*, with the remark: 'Pour donner une idée de ce genre, nous choisirons les espèces suivantes', and then lists the species under consideration along with the Tertiary species *Zamites epibius* Saporta[15], and others of Mesozoic age.

Genus CYCAS Linnaeus

CYCAS FUJIIANA Yokoyama, Jour. Coll. Sci. Imp. Univ. Tokyo **27²⁰**: 4. *pl. 1, f. 7.* 1911. (Plate 12)

> *Locality:* Manda, Miike coal field, Kiushiu, Japan.
> *Latitude:* N. 33°.
> *Geological horizon:* Eocene (Paleocene?).

The figure that serves to illustrate the description of this species may be seen to represent a cycad that is so closely similar to the existing *Cycas revoluta* Linnaeus as to be almost indistinguishable from it, as far as is indicated by form and general surficial features; and in this connection it is

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[14] KRÄUSEL, RICHARD. Senckenbergiana **10**: 105. 1928.
[15] See this paper, p. 178, Pl. 13, fig. 2.

of interest to note that *Cycas revoluta* is an element in the existing flora of
Japan at about the same latitude as that in which the fossil species was
found. Also this is the furthest north, in any part of the World, at which
any existing species of the Cycadaceae is native.[16] There are none in Eu-
rope; and in North America the nearest approach is represented by the
genus *Zamia* in northern Florida and *Dioön* in northern Mexico, at ap-
proximately latitude N. 31° and N. 30°, respectively.

Old World—Southern Hemisphere
Genus ANOMOZAMITES Schimper

ANOMOZAMITES MUELLERI Ettingshausen, Denkschr. K. Akad. Wiss.
Wien Math. Naturw. Cl. 53: 89. *pl. 8, f. 19–22.* 1887; translated by the
author in Mem. Geol. Survey New South Wales (Paleontol. No. 2), p.
94. *pl. 8, f. 19–22.* 1888. (Plate 13, fig. 3[19–22])

Locality: Vegetable Creek, near Emmaville, New South Wales, Australia.
Latitude: S. 29°.
Geological horizon: Lower (?) Eocene.

The five figures included in our figure 3, are tracings of the five figures
of the specimens depicted by Ettingshausen (*loc. cit.*) to illustrate the de-
scription of this species. The numbers 19–22 are the figure numbers on his
plate 8. Figure 20a is an enlarged representation of two contiguous pinnae
or leaflets. The other figures represent specimens natural size. Figure 22
is described by the author as showing an early state of development of a
leaf, and figures 19, 20 and 21 as distal and proximal remains of mature
leaves.

The venation, as depicted, is that of a cycad, but the general appear-
ance of the leaf may be regarded as somewhat suggestive of a fern; and
Kräusel[17] remarked, in his discussion of the species; 'Ob nicht vielleicht
doch eine Dicotyledone oder gar ein Farn vorliegt, könnte nur durch
erneute Untersuchung des Originals aufgeklärt werden'.

Ettingshausen did not attempt any comparison with any existing or
Tertiary cycad, but remarked (*loc. cit.*, p. 95) that 'one species, however,
from the Cretaceous of North Greenland, described by Heer,[18] shows by

[16] I am indebted to Dr. Matajiro Yokoyama, of the Imperial University of Tokyo,
for the following memorandum: "In the neighborhood of Tokyo *Cycas revoluta* is never
seen wild, but south of it [35°] the plant is cultivated in gardens and thrives well. It is
wild, perhaps, only in the southern part of Kyushu [Kiushiu]. Some tropical plants,
such as *Livistonia* and *Ficus Wightiana* come up to the southern ends of Kyushu
[31°] and Shikoku [33°]." A.H.

[17] KRÄUSEL, RICHARD. Senckenbergiana 10: 105. 1928.

[18] Note. The only Cretaceous species of *Anomozamites* described by Heer from

its nerves, in some degree oblique to the rachis, a remarkable and specific relation to the fossil from the Eocene beds of Vegetable Creek.'

DISCUSSION

Tertiary cycads. The type of vegetation represented by the Cycadales or, to use a broader and more comprehensive term, the Cycadophyta, reached its maximum of development, biologically and numerically, in early Mesozoic time, during the Jura-Trias period, when it was, apparently, the most conspicuous and abundantly represented type in the World's vegetation. Remains of cycadophytes have been found in deposits of Triassic and Jurassic age in arctic and antarctic as well as in intermediate regions, indicating that during that time uniform tropical or subtropical climatic conditions prevailed throughout the World, from pole to pole.

At about the beginning of the Cretaceous period, coincident with the advent of the angiosperm type of vegetation, the cycadophytes began to wane numerically and to become more restricted in their distribution until, at the close of Mesozoic time, they represented a relatively unimportant element in the then existing flora.

In early Neozoic time cooler climatic conditions than had previously prevailed began to be clearly manifested in the polar regions. Climatic zones were definitely established. New types of vegetation were evolved, and any type that could not adapt itself to the changed conditions was either exterminated or was gradually driven further and further toward the equatorial region. The cycadophytes disappeared entirely as elements in the vegetation of the boreal and austral zones; and they made their last bid for existence in the temperate zones during Eocene and Miocene time, in certain regions or localities where favorable conditions still obtained. Any definite record of any Pliocene cycad north or south of the tropical zone is lacking. The advancing cold, that culminated in the wide-spread polar glaciation of the Quaternary period, and the contemporaneous increase in local glaciation elsewhere, ultimately resulted in the extermination of all species that could not migrate and join their relatives in the tropics.

In the New World well defined foliaceous remains of Tertiary cycads have been found, all apparently referable to the existing genera *Ceratozamia*, *Dioön*, and *Zamia*, and each in the region where it would be logical to expect it, in accordance with its existing area or range of distribution. The climatic conditions on the North American continent in early Terti-

Greenland, as far as I am aware, is *A. cretaceus* (Flora fossilis arctica 3²: 70. *pl. 16*, *f. 19, 20*. 1874). This species, however, is represented by a small pinnatifid leaf or frond with forked veins. A.H.

ary (Eocene) time were apparently comparable, in certain respects, with those of today, as far as may be inferred from what records we have of the distribution of cycads at that time.

Any remains identified as those of cycads have not, as yet, been recorded from any Tertiary deposits in the north-central or eastern part of the North American continent; but from the early Eocene of the lower Mississippi valley, between latitudes 32° and 35°, three species of *Zamia* have been described, and from the Eocene of the Pacific Coast region in southeastern Alaska, at about latitude 57°, one species of *Ceratozamia* and two of *Dioön* are recognized. From these facts we may infer that the climate of the Pacific Coast at that time was milder than in the interior of the continent or eastward, as is the condition that obtains today.

Distribution of New World Tertiary cycads

CERATOZAMIA WRIGHTII n. sp.............................Alaska. N.Lat.57°.
DIOÖN INOPINUS n. sp...................................   "   "   "   "
D. PRAESPINULOSUM n. sp...............................   "   "   "   "
CYCAD (gen. et. sp.?)..................................California. N.Lat.35°25'.
ZAMIA TENNESSEEANA Berry............................Tennessee. N.Lat.35°15'
Z. MISSISSIPPIENSIS Berry.............................Mississippi. N.Lat.32°21'.
Z. (?) WILCOXENSIS Berry.............................Louisiana. N.Lat.32°3'.
Z. COLLAZOENSIS Hollick...............................Porto Rico. N.Lat.18°
Z. NOBLEI Hollick.....................................Porto Rico. N.Lat.18°.
Z. species, Berry.....................................Colombia. N.Lat.5°.
Z. PRAECEDENS Ettingshausen..........................Brazil. S.Lat.12°.
Z. TERTIARIA Engelhardt...............................Chile. S.Lat.37°.
Z. AUSTRALIS Berry....................................Argentina. S.Lat.41°.

The advancing cold, that culminated in the almost complete glaciation of the northern part of the continent in the Quaternary period drove the last remaining species of *Ceratozamia* and *Dioön* southward along the Pacific coastal region to where we now find the existing species of these genera, in Mexico. When and where they were last in existence in the intermediate region we have no available records; but we may be justified in assuming that they represented an element in the Miocene flora of the region, especially as cycads are known to have been in existence in Europe and possibly also in South America in what are now temperate latitudes, until about the middle of the Tertiary period.[19]

In the North American continental interior, and eastward, the cycads had been driven southward some time previously, to the Mississippi em-

[19] *Note.* After this was written I received from Dr. C. D. Hanna, Curator, Department of Paleontology, California Academy of Sciences, specimens that represent undoubted remains of cycads, recorded as Miocene in age, from Kern County, California (see page 172).

bayment, where at least three species of *Zamia* continued to exist until early Tertiary time. Apparently, however, conditions became more and more unfavorable. The limit of further southward migration had been reached and the genus was exterminated as an element in the continental flora of North America, until it subsequently returned by way of the Florida peninsula, where it's descendents now form a characteristic element in the existing flora.

Further southward, to the Equator and beyond, at least as far as south latitude 41°, some half a dozen specific representatives of the genus *Zamia* have been recorded as elements in the Tertiary floras of the Antillean region and South America. During that period, apparently, it was the dominant cycad genus of the New World, as it is at the present time.

In Europe the east-west direction of the principal mountain systems —the Pyrenees, Alps, Karpathians, etc.—and the Mediterranean Sea, formed impassable barriers to southward migration when driven in that direction for refuge from the constantly advancing cold of the Tertiary period.

A number of described species, based upon remains of leaves, fruit, trunks, etc. (described under the generic names *Zamites*, *Zamiphyllum*, *Zamiostrobus*, *Ceratozamites*, *Cycadites*, etc., in accordance with their apparent generic relationships), all more or less similar in surficial characters to similar parts in existing genera, were able to maintain their existence in Europe until about the middle of the Tertiary period. Their last known stand in the western part of the continent was made in the south of France, where the Pyrenees Mountains and the Mediterranean Sea barred them to the south, and these generic types were there exterminated. Further eastward the Alps, Karpathians, Balkans, and Caucasus Mountains formed equally impassable barriers, and there also the extermination was complete. In Greece, however, further to the south, a species of *Encephalartus* continued to exist for a while, after its other European relatives had perished. There was, apparently, more direct land connection at that time than now, between Greece and Africa, and although the genus finally became extinct in Europe, by reason of general climatic change, it had in the meantime become established southward, where its representatives compose the most extensive of the two existing cycad genera native in Africa. This genus may be regarded as satisfactorily identified in connection with the fossil species of Greece; but the generic affiliations of most of the other described European Tertiary species may be regarded as not satisfactorily determined and, in connection with certain of them, relationship with the cycads in general appears to be open to question.

In Asia only one discovery of a Tertiary cycad has thus far been re-

corded—a well defined species of *Cycas*, in Japan. If any others were in existence at that time in the interior of the continent we may infer that they met with a fate similar to that which befel their contemporary relatives in Europe, by reason of similar east-west trends of many of the mountain ranges. The north-eastern part of the Asiatic continent, however, in common with the northwestern part of the North American continent, was not subjected to glaciation such as that which prevailed in Europe and in northern and eastern North America during the Quaternary period, although evidences of severe cold are manifest. Along the eastern coast, however, through Japan, China and the Malay peninsula a route for southern migration was open, of which representatives of the genus *Cycas* took advantage and subsequently returned by it to southern Japan when favorable climatic conditions were again established.

The only recorded Tertiary cycad from south of the Equator in the Old World is the more or less problematic *Anomozamites Muelleri*, described by Ettingshausen, from Australia. If this is a cycad it may represent an insular generic type, now extinct, which can not be satisfactorily compared with any now in existence.

Distribution of Old World Tertiary cycads

ZAMIPHYLLUM SAMBIENSE (Caspary) Caspary & Klebs. . . . Germany. N.Lat.54°50'.
ZAMITES PALEOCENICUS Saporta & Marion. . . . . Belgium. N.Lat.50°45'.
Z. (DIOÖN) TERTIARUS Heer. . . . . Switzerland. N.Lat.46°30'
Z. RACZKIEVICZII Stur. . . . . Hungary? N.Lat.46°?
Z. EPIBIUS Saporta. . . . . France. N.Lat.43°45'.
ZAMOIOSTROBUS SAPORTANUS Schimper. . . . . France. N.Lat.43°.
BUCKLANDIA NIERSTEINENSIS Kräusel. . . . . Germany. N.Lat.49°45'.
CYCADITES? ESCHERII Heer. . . . . Switzerland. N.Lat.47°45'.
CERATOZAMIA HOFMANNI Ettingshausen . . . . Austria. N.Lat.47°30'.
CERATOZAMITES VICETINUS Meschinelli. . . . . Italy. N.Lat.45°30'.
ENCEPHALARTUS GORCEIXIANUS Saporta. . . . . Greece. N.Lat.38°20'.
CYCAS FUJIIANA Yokoyama. . . . . Japan. N.Lat.33°.
ANOMOZAMITES MUELLERI Ettingshausen . . . . Australia. S. Lat.29°.

Existing cycads. The existing cycad flora is included in nine genera. The dominant genus in the New World is *Zamia*, with about thirty species and with a geographic range that extends from N. Lat. 31° to S. Lat. 22°. The outstanding genus in the Old World is *Cycas*, with about twenty species and a range that extends from N. Lat. 35° to S. Lat. 35°. These two are the only genera that cross the Equator and are common to both the Northern and the Southern Hemisphere. No genus of the Cycadaceae is common to both the Eastern and the Western Hemisphere. All of the genera are tropical or subtropical in their distribution.

The salient facts in connection with the distribution of the nine re-
cognized genera may be tabulated as follows:

Genera	Number of species	Distribution	Latitude (approximate)
ZAMIA L.	±30	Florida, West Indies, Central and South America	N.31°–S.22°
DIOÖN Lindl.	± 4	Mexico	N.30°–N.17°
CERATOZAMIA Brongt.	± 6	Mexico	N.25°–N.17°
MICROCYCAS A. DC.	1	Cuba	N.22°
BOWENIA Hook. f.	2	Northeastern Australia	S.25°–S.15°
MACROZAMIA Miq.	±15	Australia	S.35°–S.15°
ENCEPHALARTUS *fide* Steud. (=ENCEPHALARTOS Lehm.)	±15	South Africa	S.35°–S.20°
STANGERA *fide* Voss (=STANGERIA T. Moore)	1	South Africa	S.32°–S.23°
CYCAS L.	±20	Japan, southern China, East Indies, Australia, islands of the Pacific and Indian Ocean (and east Africa?).	N.35°–S.35°

With the exception of *Zamia* and *Cycas* it may be noted that the genera
are remarkably local and restricted in their distribution. *Dioön* and *Cerato-
zamia* are confined to Mexico; *Microcycas* to Cuba; *Bowenia* and *Macro-
zamia* to limited regions in Australia; *Encephalartus* and *Stangera* to South
Africa. Furthermore they do not occur as pure stands or extensive aggre-
gates but only in scattered groups or as individuals. Incidentally, also,
two of the genera—*Microcycas* and *Stangera*—are monotypic, and one
other—*Bowenia*—is represented by but two species. These three genera
are obviously on the verge of extinction, and all of the others, with the
exception of *Zamia* and *Cycas*, are so local and restricted in their distri-
bution that a relatively slight environmental change, whether brought
about through geologic or through human agency would, probably, result
in their extermination.

SUMMARY AND CONCLUSIONS

Tertiary cycads are of special interest as representing the last bid for
life of the cycadophytes outside of the tropical and subtropical zones as
now recognized; they are identical or closely related generically to those
now in existence in the tropics and subtropics; the close similarity be-
tween the fossil and the existing forms indicate that tropical or sub-
tropical conditions prevailed in Tertiary time in the regions where the
fossil forms are found; the existing cycadophytes represent the remnants of

a formerly widely distributed type of vegetation which may be regarded as approaching extinction, due, primarily, to unfavorable environmental and climatic changes over extensive areas of former occupation.

THE NEW YORK BOTANICAL GARDEN

Description of plates 1–14

PLATE 1

PLATE 8

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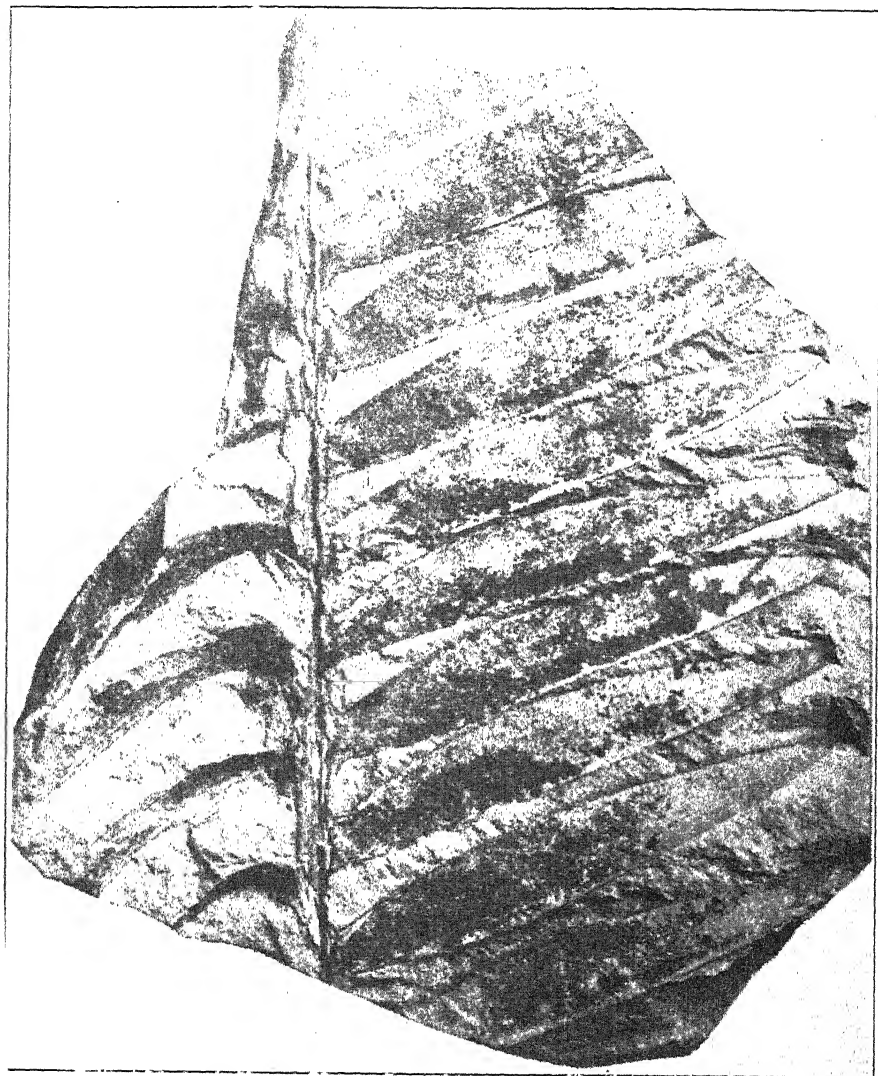
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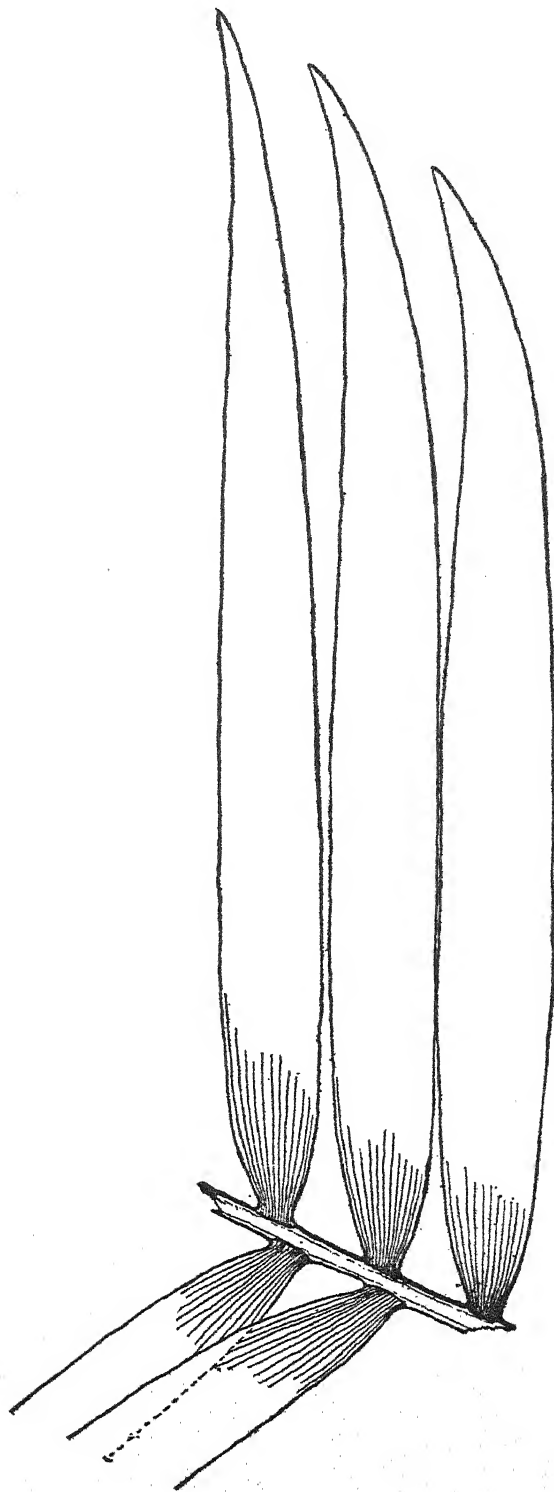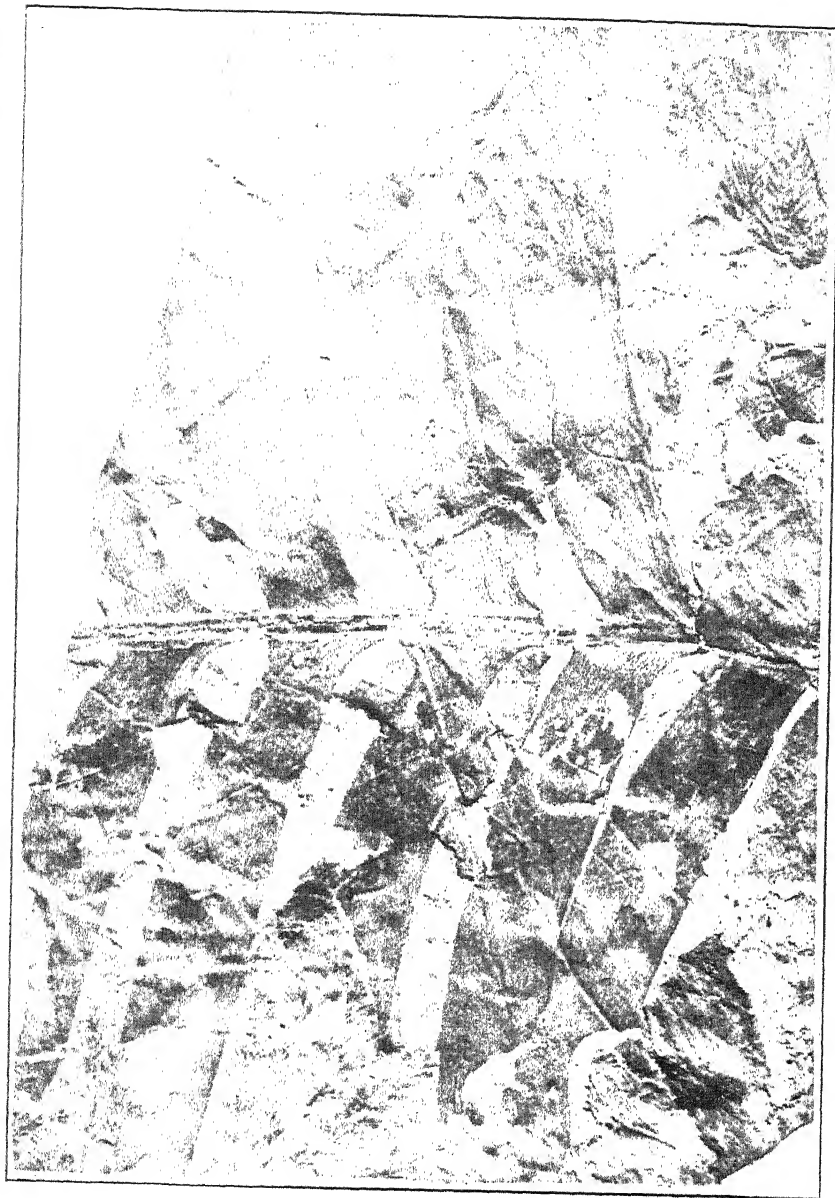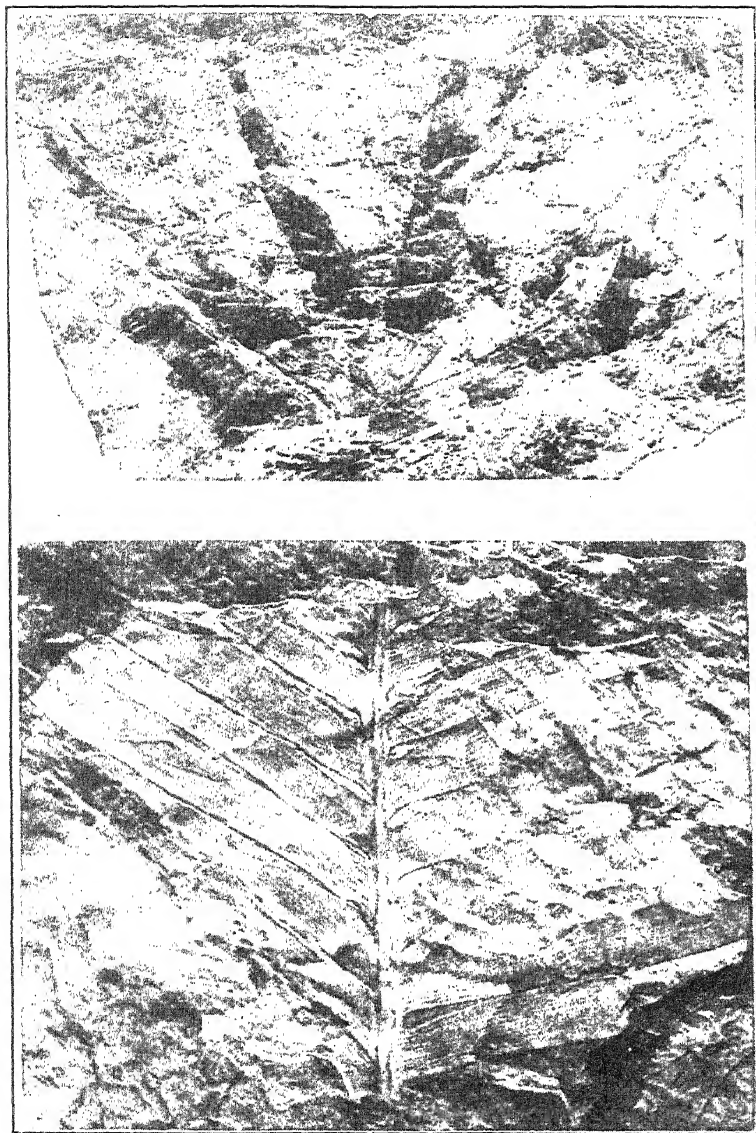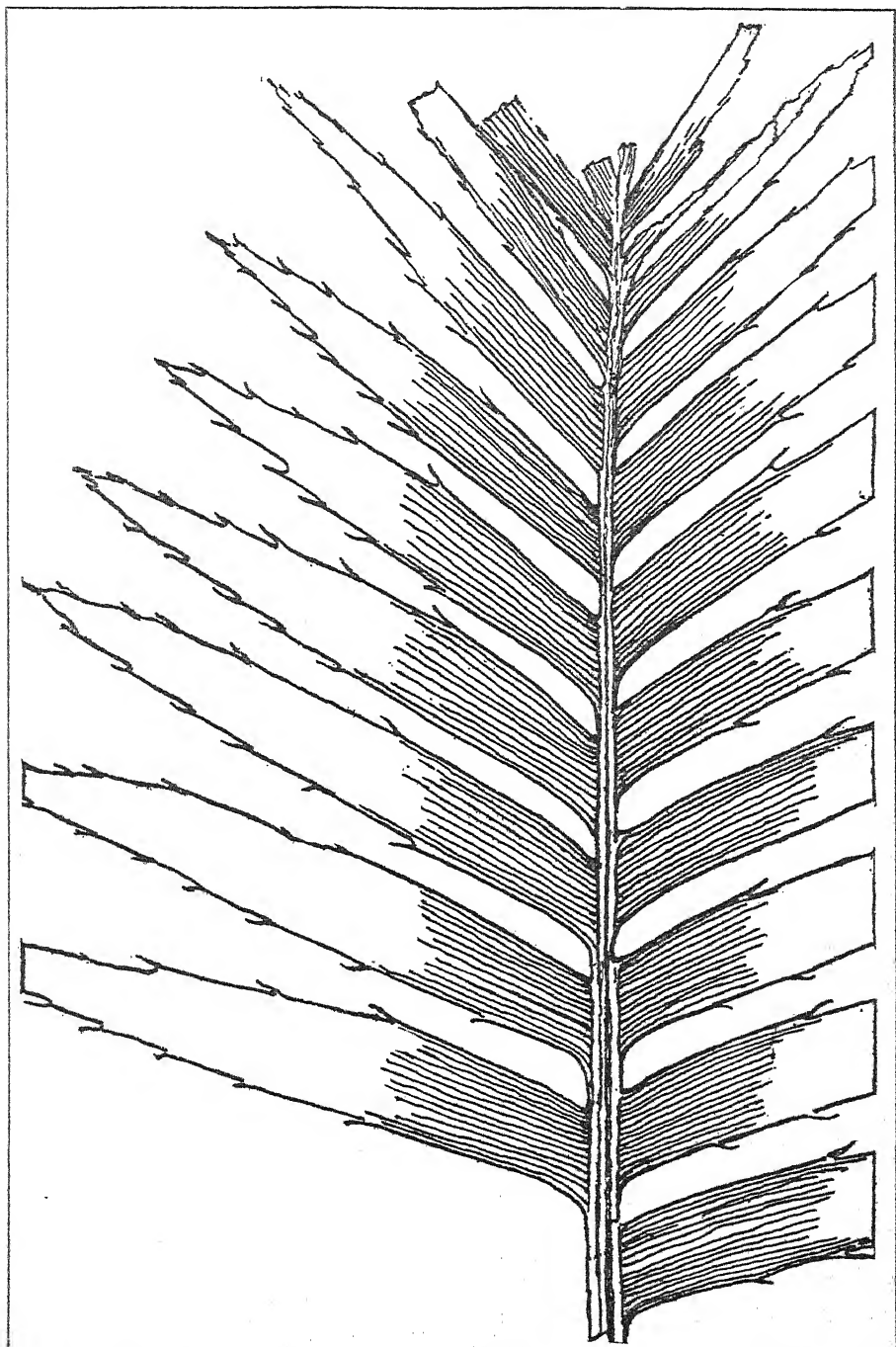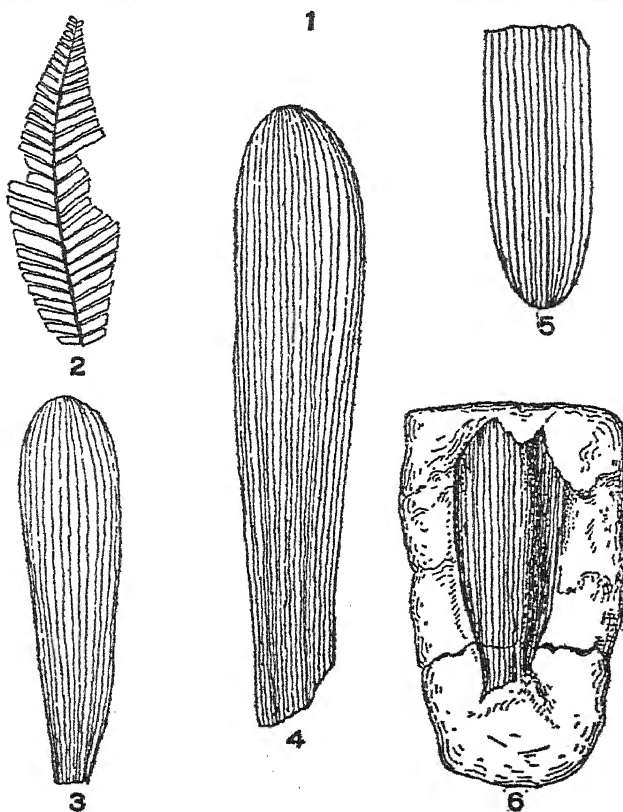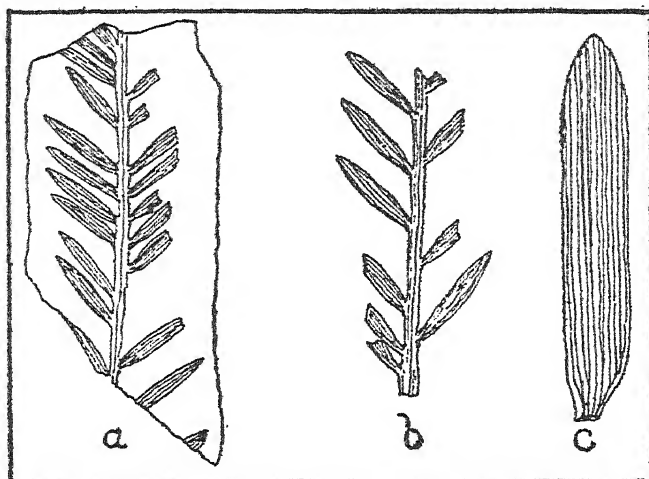
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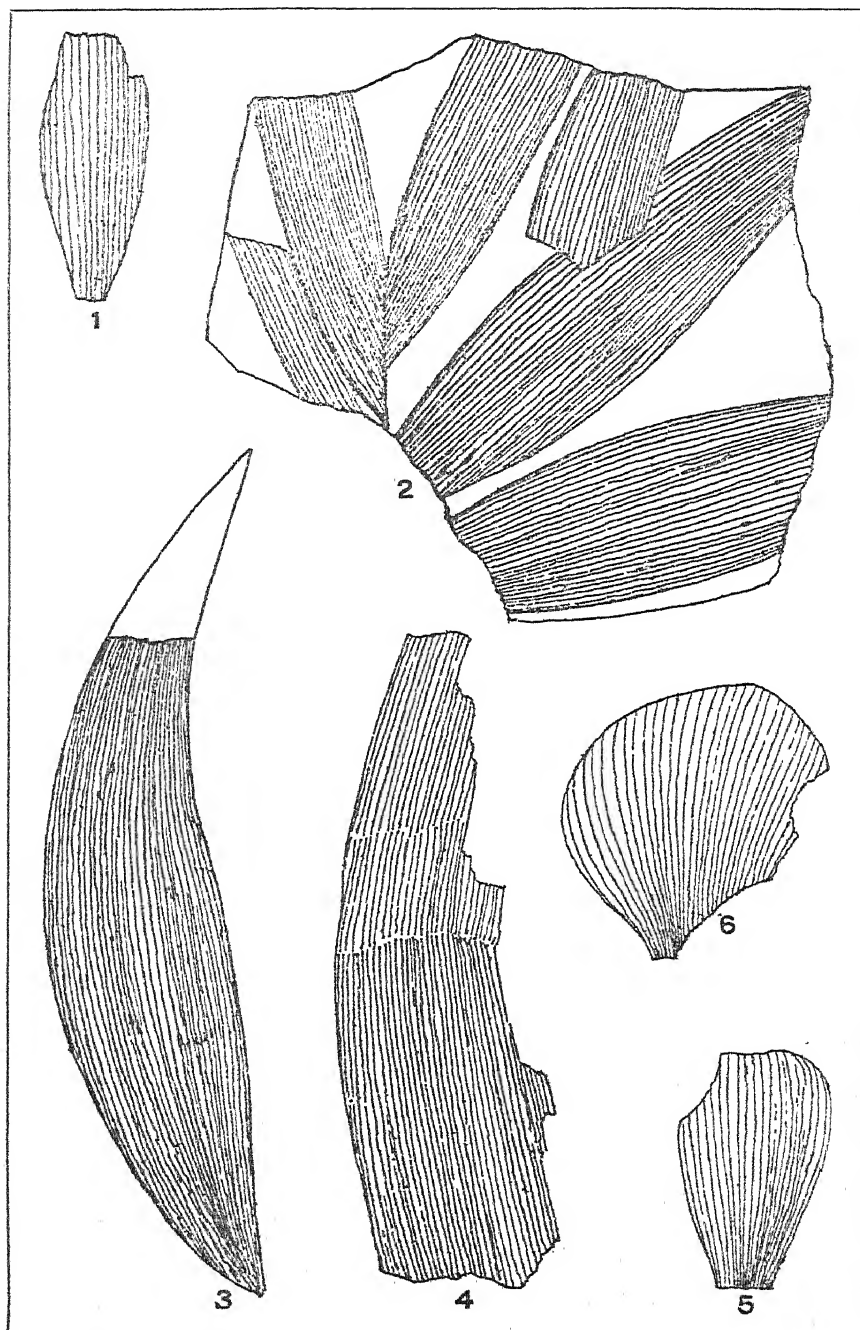
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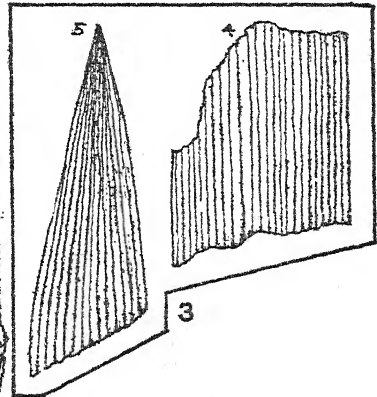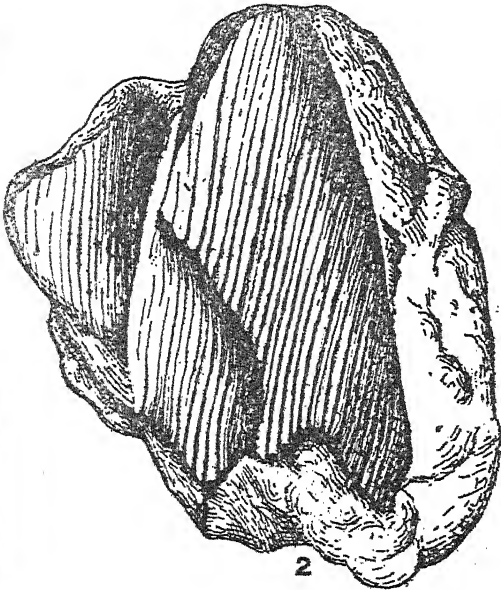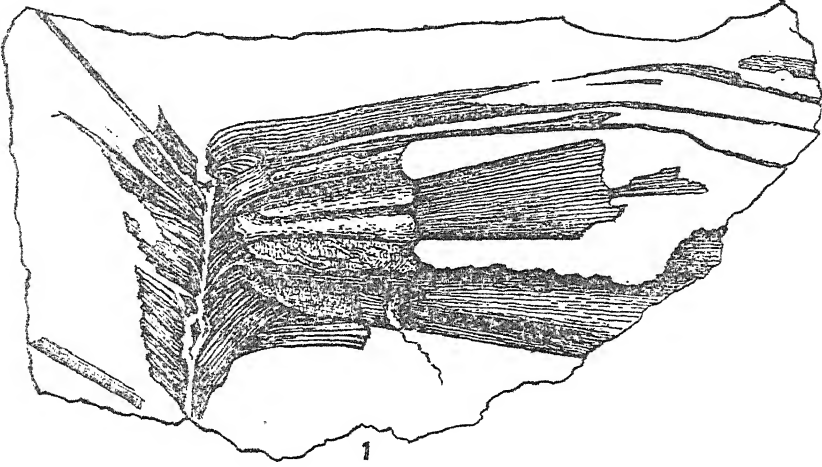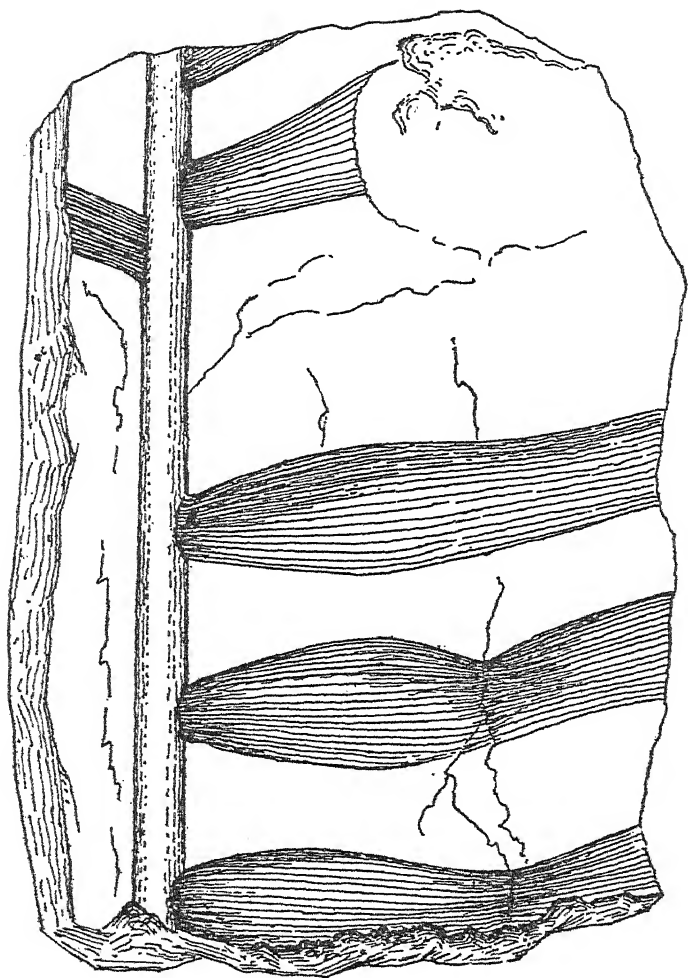
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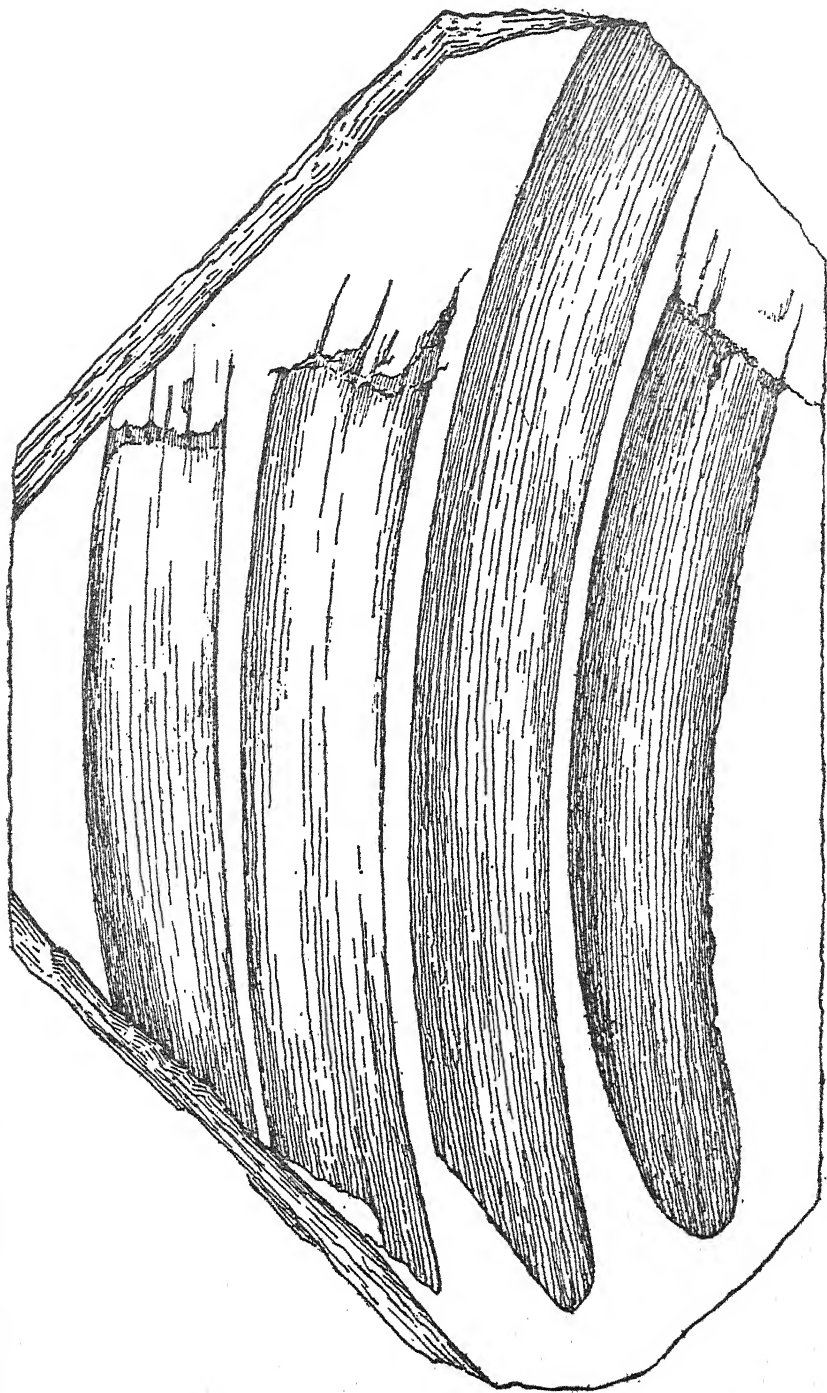
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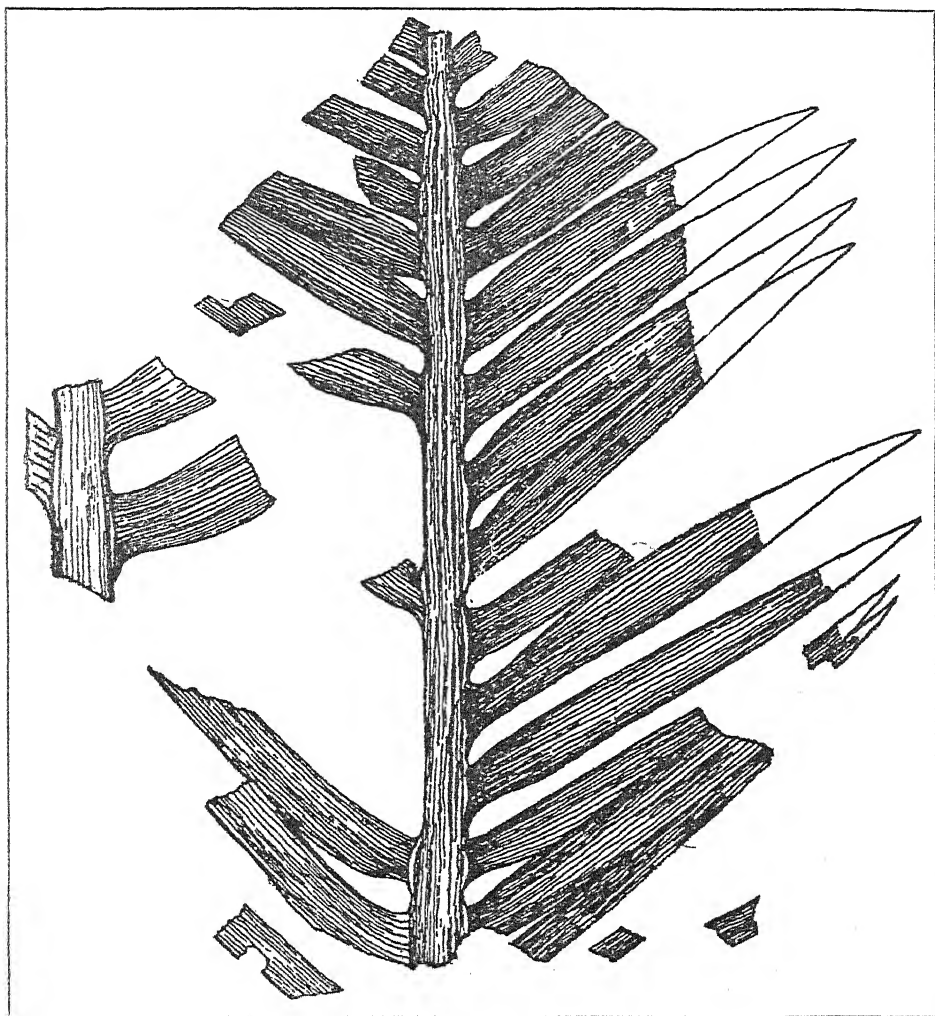
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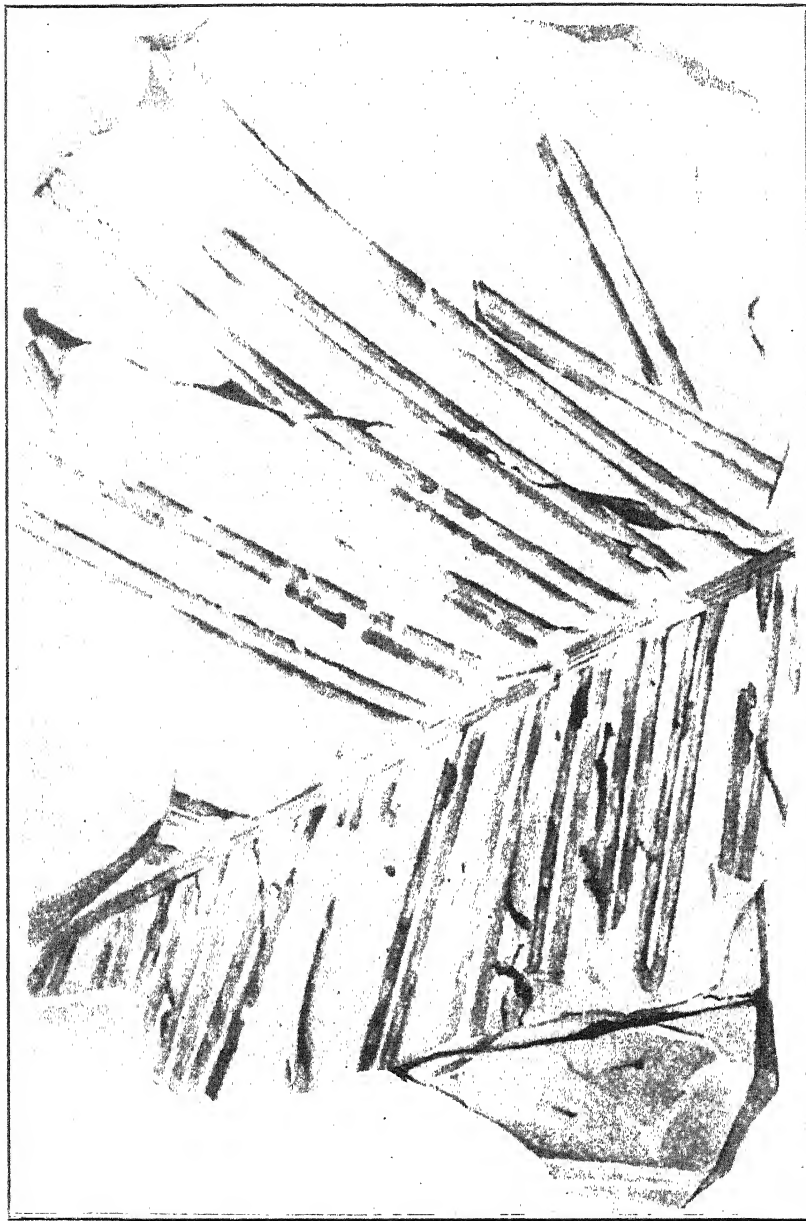
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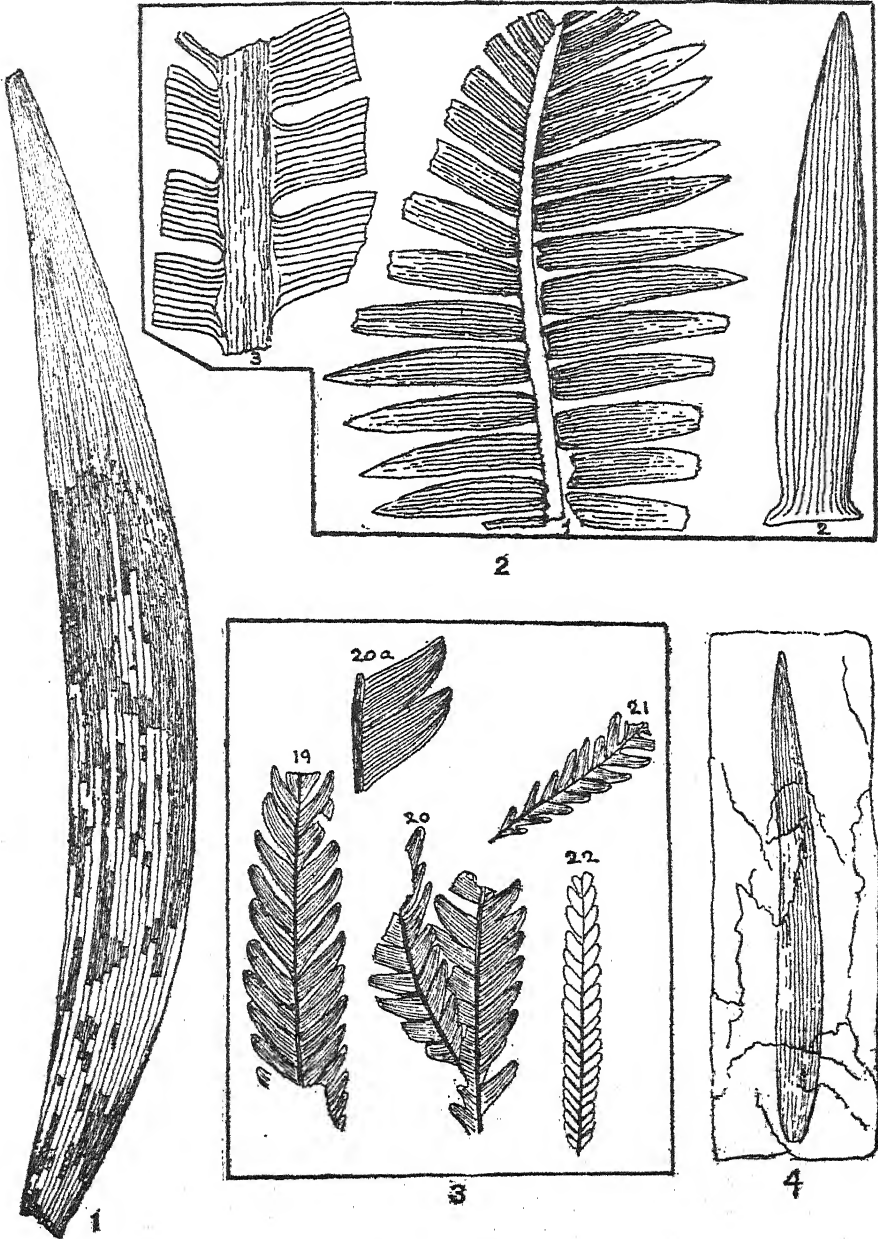
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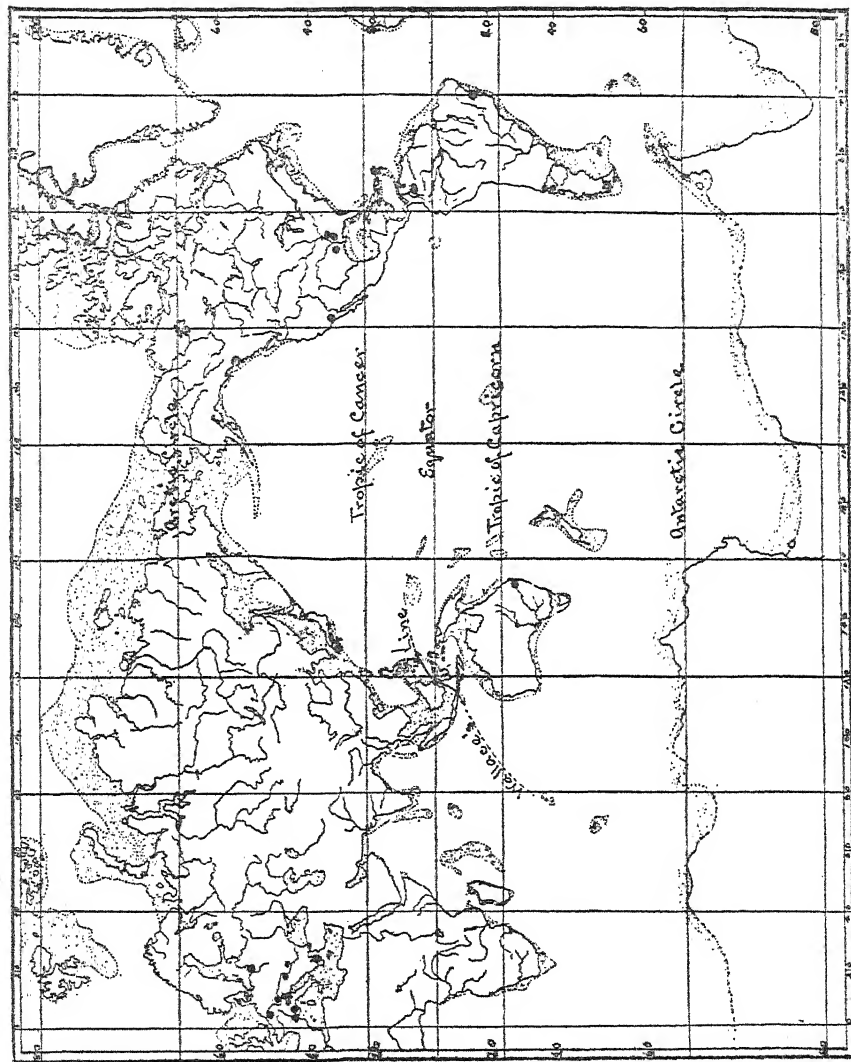
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Inhibiting influence of colloidal starch, inulin, and agar on the stimulation of Aspergillus niger by zinc sulphate

KATHARINE BROWNE STEHLE

(WITH FOUR TEXT FIGURES)

Though a great deal of work has been done upon the growth and stimulation of *Aspergillus niger* in various media, and with various stimulants, little has been done with a colloidal substance present in the solution, either as carbohydrate source, or as an auxiliary substance. The presence of such a substance seems to alter the reaction of the fungus to an inorganic poison such as zinc sulphate.

Kunkel (1913) attempted to determine the toxicity of salts to *Monilia sitophila* in the presence of certain organic substances such as starch, peptone, glucose, fructose, and galactose. He found that the concentrations at which various salts are toxic to *Monilia* depend on the kind of organic substances contained in the media to which the salts are added. The same salt, he said, may be highly toxic in one medium, but quite harmless in another. He did not, however, offer any explanation for this difference in toxicity of the salts in various media.

One of the first experimenters on the effect of metal salts on the growth of *Aspergillus niger* was Raulin (1869). He observed that increased growth resulted when various metallic salts, among them those of zinc, were present in the culture medium. From this he concluded that these elements were all indispensable for normal development of the fungus. Richards (1897) carried on numerous experiments testing the effects of various salts of heavy metals and some organic compounds on the growth of *Aspergillus niger*, *Penicillium glaucum*, and *Botrytis cinerea*. He concluded that these substances were not indispensable to the fungi, but were rather agents which by chemical stimulation caused an acceleration in growth. Steinberg (1919) considered that the greater acidity of the medium due to the presence of the heavy metal ions might possibly explain the increase in growth obtained with zinc salts present. Zinc sulphate is by him, in accordance with the results obtained by Richards, Fred (1911), and other workers, considered as a chemical stimulant causing unusual growth.

The object of the experiments reported in the present paper was to find out whether, when a colloid is present, or when the carbohydrate is presented in starvation quantities, the zinc sulphate has any effect on the dry weight of the yield of mycelium, or whether the amount of zinc sulphate which can be tolerated by the fungus is in any way altered.

METHODS

The methods used in these experiments were similar to those of others who have worked on the stimulation of *Aspergillus*. Pyrex glass-ware was used. Steinberg (1918) concluded that, since cultures of *Aspergillus* grown in Pyrex glass were lower in weight than those grown in other kinds of glass, the Pyrex glass does not add any stimulant, such as zinc, to the solution. The glass-ware that came in contact with the culture solutions was soaked at least overnight in a cleaning solution (sodium dichromate and sulphuric acid), then rinsed thoroughly in tap water, then twice in distilled, and once in double-distilled water. The materials used for the culture solutions were the 'Reagent' grade of Merck's chemicals, with the exception of the starch, inulin, sugar, and agar. Of these last mentioned, the starch and inulin were the 'improved Pfansteil' of the Special Chemicals Company, the sugar was the crystalline form of Kahlbahn's, and the agar 'Difco' standardized. Double-distilled water was used in all cases, the second distillation being through a quartz tube.

The culture medium used was that known as the Pfeffer's solution, containing .5 per cent potassium phosphate (monobasic), .25 per cent magnesium sulphate ($MgSO_4$ 7 H_2O), and 1 per cent ammonium nitrate. Iron is needed only in very small quantities; no iron salt was specially added, as it was assumed that sufficient amounts of iron salts might be present as an impurity in the three main salts. Various concentrations of carbohydrate were used. In making up the culture medium, the solutions were sterilized in an Arnold steam sterilizer, the sugar solutions for thirty minutes, the solutions containing agar for an hour. This was necessary in order to dissolve the agar. The starch and inulin solutions were made by mixing a small amount with water, and then adding this slowly to the culture medium which was boiling. Fifty cubic centimeters of medium were placed in each culture flask (150 cc. Erlenmeyer).

Zinc sulphate was added, for the stimulation series, in fractions of a volume-normal solution. For each series double-distilled water was added to the control, and to each of the flasks containing lower concentrations of the stimulant, so that there would be an equal volume for every flask. In the cases where it would have been necessary to add 2 cc. or more, the nutrient solution was made up double strength, and 25 cc. were put in each flask. The remaining 25 cc. were added by using the desired proportions of normal zinc sulphate and double-distilled water.

The stock cultures of *Aspergillus niger* were grown on white bread, sterilized for half an hour in the Arnold sterilizer before being inoculated. For inoculating each culture flask two loopfuls of spores were taken from the stock culture with a platinum needle.

The cultures were incubated at a temperature of 34.5°C. for four days. Notes were taken at the end of that time on the macroscopic appearance of the felts, fruiting, folds in the felts, yellow coloration, etc. The mycelial felts were then placed on weighed filter-papers, washed with distilled water, and dried in a hot-air oven at 60° for three days. If the dried felts and papers could not be weighed immediately, they were removed to a calcium chloride dessicator. In the cases where the felts were not complete, and therefore could not be removed from the liquid in one piece, the contents of the culture flask were put through the filter paper. In the case of the solutions containing agar, it was found that none of the agar went through the paper, and therefore the weights were correspondingly higher. In all the cultures that were reaped with the medium, 125 mg., the amount of agar allowed for each culture flask when the series were set up, was subtracted from the weight to allow for this. It was also found, by weighing five filter papers before and after they had been in the drying-oven for three days, that the papers lost an average of 15 mg., due to water content, which amount was added to all the averages.

EXPERIMENTAL RESULTS

It was first noticed that, using a 3 per cent starch solution, the macroscopic appearance of the felts was hardly different for those grown with, and those grown without zinc in the medium. Other observers have found, using sugar alone as the carbohydrate, that the external appearance of the fungus mycelium is greatly altered by the presence of small amounts of inorganic stimulants, such as zinc sulphate. Richards (1910) has described this appearance as follows:

> Fungi commonly cease to form conidia under stimulation; and mycelial felts are buckled and knotted instead of being flat and even and their consistency is different, being tough and leathery instead of somewhat tenuous in texture as in the normal growth.

In the case of cultures grown with 3 per cent starch as the carbohydrate, (table 2) however, the felts, on an average, fruited almost as well, at least, as the control up through a concentration of .009 N zinc sulphate. The abundance of spore production then decreased with higher concentrations, down to none in most cases at .031 N and .036 N. Richards (1897) reported that, using 5 per cent sugar as carbohydrate source, with a concentration of .0001 N zinc sulphate present, conidia ripened two days later than in the zinc-free solutions, and with .001 N zinc sulphate, spore formation did not occur at all. In the starch series, all but the control cultures showed some folds in the felts (table 3), but these were almost negligible compared with the folds of a stimulated felt grown in a nutrient

solution containing sugar. The consistency, too, of the mycelium was different, the starch felts being soft and pliable, as compared with the tough leathery felts of sugar solutions. The yellow coloration of nutrient solution found by Richards (1897) to occur usually in the presence of zinc was not constant either for stimulated or control felts.

A comparison may be made of the results obtained from series with 3 per cent starch (table 14) and 3 per cent sugar (table 12) in the nutrient solution, and with various concentrations of zinc sulphate present. The dry weight of fungus obtained in each case in the control solution was practically the same. It may be then that sugar and starch were of like

TABLE 1

Effect of different carbohydrates in the culture medium on the growth stimulation of Aspergillus niger by zinc sulphate

CARBOHYDRATE		HIGH-POINT	INCREASE OVER CONTROL	.0005 VS. CONTROL	
Sugar	.25%	.0001 N	6.5%	Decrease	23.4%
Sugar + Agar	.25%	Control	—	"	24.7%
Sugar	.5 %	.0003 N	12.9%	"	2.5%
Sugar + Agar	.5 %	.002 N	23.5%	"	7.3%
Sugar	1 %	.004 N	2.3%	"	10.5%
Sugar + Agar	1 %	Control	—	"	6.8%
Sugar	1.5 %	.002 N	73.2%	Increase	61.1%
Sugar	2 %	.0003 N	58.2%	"	52.2%
Sugar	3 %	.0003 N	47.4%	"	40.7%
Sugar + Agar	3 %	.027 N	24.1%	"	16.4%
Starch	3 %	.001 N	14.3%	"	5.6%
Inulin	1 %	.018 N	15.5%	"	9.0%

value as an energy source for *Aspergillus*, and so the results of using these two nutrients may be compared with fairness. If the curve of dry weight plotted against concentration of zinc sulphate (fig. 1) be compared for these two, it will be seen that both rise with increased amounts of zinc sulphate, with the high point for 3 per cent sugar at .0003 N, and for 3 per cent starch at .001 N. In the case of the sugar series, however, the percentage increase of the weight at .0003 N over that with no stimulant present, is 47.4 per cent; in the case of the starch, at the high point it is only 14.3 per cent. In both cases there is a slight drop in yield at .002 N; but for higher concentrations the curves differ markedly in slope. The sugar curve drops off definitely and gradually to a point between .04 N and .045 N, where there is no longer any growth; the starch curve, on the

other hand, is almost a straight line over a wide range of zinc concentrations, exhibiting no tendency to fall until a concentration of .031 N is reached. At .036 N the percentage decrease of the starch culture below the weight of the control is only 30.7 per cent as against 71.7 per cent for the
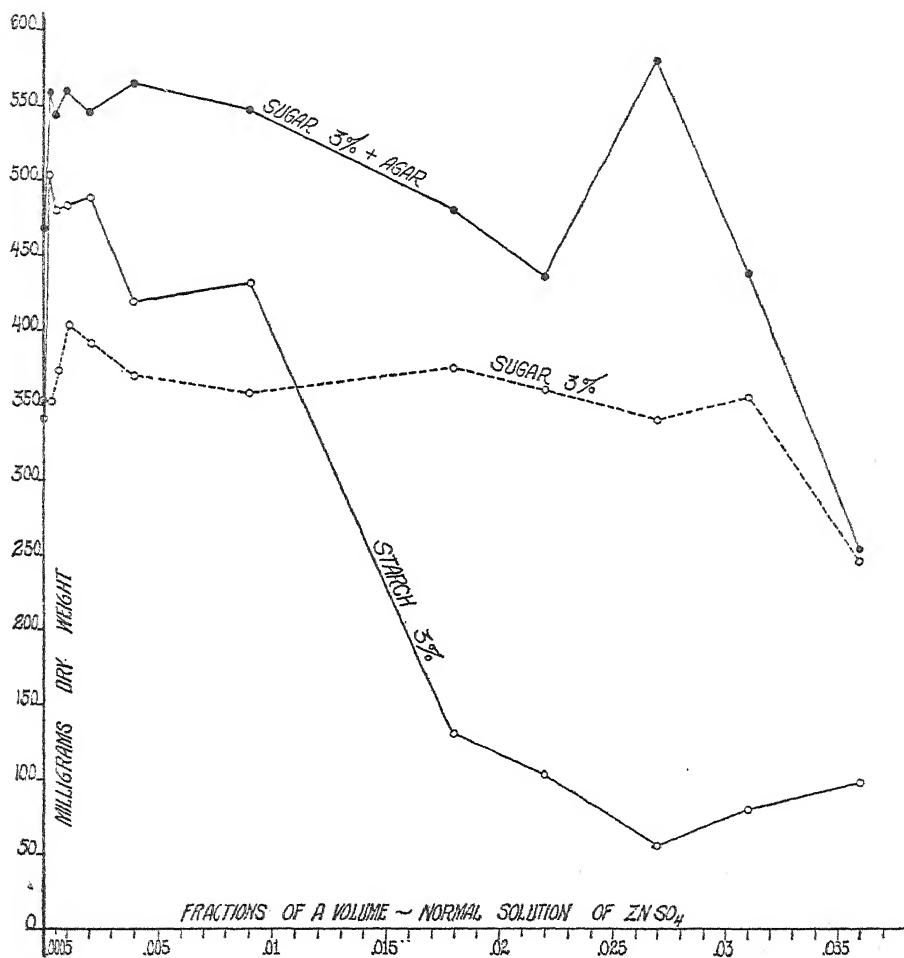
Fig. 1. Growth of *Aspergillus niger*, as influenced by ZnSO₄, using 3% sugar, 3% starch, and 3% sugar with agar as carbohydrate.

sugar culture. These results show very clearly that the presence of colloidal starch in the culture solution had a pronounced effect in lowering the toxicity of the zinc sulphate, but no attempt was made to find the lethal concentration of zinc sulphate under these conditions. The increase over the control weight at the high point was only 14.3 per cent when

TABLE 2

Macroscopic appearance of felts: fruiting

CARBOHYDRATE	GOOD FRUIT	SOME FRUIT	LITTLE FRUIT	NO FRUIT
Sugar .25%	Control—.002			
Sugar .25% + Agar	Control—.036			
Sugar .5%	Control—.002			
Sugar .5% + Agar	Control—.022	.027	.031	.036
Sugar 1%	Control	.0001—.002	.004	.009 & higher
Sugar 1% + Agar	Control—.099	.018, .022, .027		.031 & higher
Sugar 1.5%	Control	.0003	.0005—.002	
Sugar 2%	Control		.0005,.0003,.002	
Sugar 3%	Control		.0001	.0003 & higher
Sugar 3% + Agar	Control		.0001—.004	.009 & higher
Starch 3%	Control—.009	.018—.027,	less and less	.031, .036
Inulin 1%	Control—.018		.036	

TABLE 3

Macroscopic appearance of felts: stimulation

CARBOHYDRATE	FELTS FOLDED BUT FRUITING	'REAL STIMULATION'	YELLOW
Sugar .25%	None	None	None
Sugar .25% + Agar	None	None	1—.0001
Sugar .5%	.0003, 1—.0005, .002	None	None
Sugar .5% + Agar	5—.0001, 3—.0003, 4— .0005, .001, .002, .027, .031	None	None
Sugar 1%	All but control up to .009	.009 to end	One control, one or two of rest
Sugar 1% + Agar	All but control	None	All in some cases
Sugar 1.5%	All but control	None	All but control
Sugar 2%	All but control	None	All but control
Sugar 3%	None	All but control	Varied
Sugar 3% + Agar	None	All but control	Varied
Starch 3%	All but control, except .0003 in some cases	None	Varied
Inulin 1%	.001—.018	None	Varied

starch was present, as compared with the increase of 94.7 per cent found by Richards (1899) using 5 per cent sugar as the carbohydrate.

Inulin in a 1 per cent solution was also used as a carbohydrate source. The effects of the colloid here may be clouded by the effects of a poor nutrient solution, which will be discussed later. Not enough series were conducted to make the results with inulin sufficiently reliable for precise conclusions. The macroscopic appearance of the felts (tables 2 and 3) was even more striking here than in the starch series; the cultures that contained .018 N or less of zinc sulphate produced as abundant conidia as did the control. At the next higher concentration tried, .036 N, there was still a slight amount of spore production. In some cases the .0005 N cul-
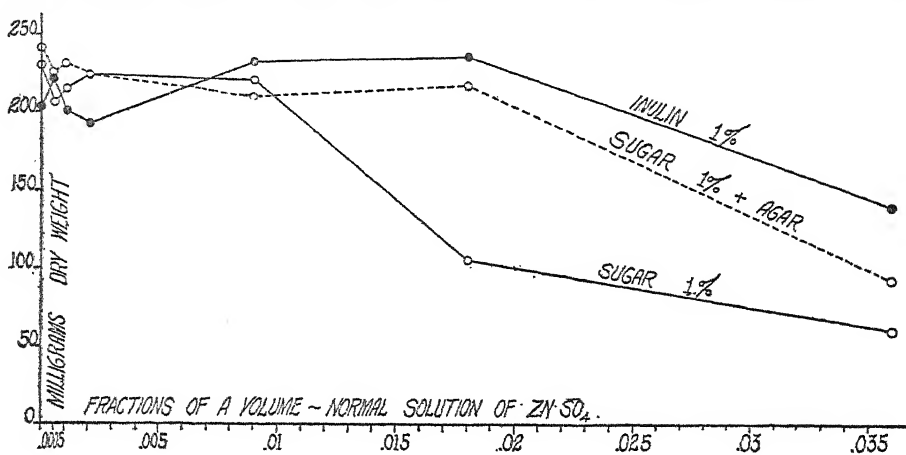
Fig. 2. Growth of *Aspergillus niger* as influenced by ZnSO₄, using 1% inulin, 1% sugar, and 1% sugar with agar as carbohydrate.

tures showed no folds; in others all the cultures containing zinc were slightly convoluted. Again, the yellow color was not a constant characteristic of either stimulated or control felts. The high point (table 15) for cultures containing this concentration of inulin was obtained with .018 N zinc sulphate; this point represents an average increase in weight over the control of 15.5 per cent (table 1). At .0005 N the increase over the control was 9.0 per cent. No attempt was made to determine the lethal point. At .036 N, the highest concentration of zinc sulphate used, there was a decrease below the weight of the control felt of only 31.2 per cent. By comparing the graphs of figure 2 showing dry weight plotted against zinc sulphate concentration for culture media containing 1 per cent inulin, 1 per cent sugar, and 1 per cent sugar with agar, it will be seen that the inulin curve follows more closely that of the sugar and agar, when the higher zinc sulphate concentrations are considered.

TABLES 4–14

Dry-weights of felts of Aspergillus niger, with zinc sulphate added to the culture medium in fractions of a Normal solution

In the following tables, to each of the final averages is added 15 mg. to allow for weight lost from the filter papers in the drying oven.

Weights marked * are those where the felts were not complete, and the weight of culture medium is included. From each of these, 125 mg. was subtracted, to allow for the weight of dried agar.

Cultures were incubated 4 days, at a temperature of 34.5°C. Weights are in milligrams.

TABLE 4
Sugar .25 per cent

−Zn	.0001	.0003	.0005	.001	.002
91			75		
93	99	64	59	95	64
107	114	79	82	110	79

TABLE 6
Sugar .5 per cent

−Zn	.0001	.0003	.0005	.001	.002
105			112		
150		146	136		106
142.5		161.0	139.0		121.0ᵃ

TABLE 5
Sugar .25 per cent, Agar .25 per cent

−Zn	.0001	.0003	.0005	.001	.002	.004	.009	.018	.022	.027	.031	.036
91	90	99	94	86	74							
106	66	93	79	115	91							
156	114	77	68	91	59	89	69	109	58	87	141	96
						88	84	98	85	90	113	66
93											128	82
											147	173
											143	147
126.5	105.0	104.7	95.3	112.3	89.7	103.5	91.5	118.5	86.5	103.5	94.4	77.8

TABLE 7
Sugar .5 per cent, Agar .25 per cent

−Zn	.0001	.0003	.0005	.001	.002	.004	.009	.018	.022	.027	.031	.036
147	136	137	131	145	148							
95	157	172	139	136	109							
126						131	131	109	111	129	146	138
						126	101	138	128	111	144	
						125	105	110	112	119	120	
240					261	199	167	187	281	210	119	279*
					141	182	200	143	139	112	336*	267*
					285							190*
												242*
142	98	141	136	147								
	148	163	164	121								
	146	114	120	141								
165.	152.	160.4	153.	153.	203.8	167.6	155.8	152.4	169.2	151.2	163.	138.2ᵃ

ᵃ15 mg. added to weight to allow for loss of weight from filter paper.

TABLE 8
Sugar 1.5 per cent

−Zn	.0001	.0003	.0005	.001	.002
183		287	304		328
198		302	319		343ᵃ

TABLE 9
Sugar 2 per cent

−Zn	.0001	.0003	.0005	.001	.002
234		379	364		378
249		394	379		393ᵃ

TABLE 10
Sugar 1 per cent

−Zn	.0001	.0003	.0005	.001	.002	.004	.009	.018	.022	.027	.031	.036	.04	.045	.05	.1	.2
171		204	225		227												
202	179			215	207	210	214	39	68	24	15	46					
216	154	163	143	161	170	207	200	120	85	77							
	150	193	178	166		244	207	100	98	86							
311	179	212	190	225	194	225	203	66	107	101	110	—					
204	197	166	214	228	193	210	199	121	123	94	50	34					
											41	37					
											166	56					
213																	
244													206	—	—		
186											36	96	—				
213											124	40	—				
180													—				
													—				
229.0	186.8	204.6	205.0	214.0	223.2	234.2	219.6	104.2	111.2	91.4	92.4	59.1	56.2	—	—	—	—ᵃ

TABLE 11
Sugar 1 per cent, Agar. 25 per cent

−Zn	.0001	.0003	.0005	.001	.002	.004	.009	.018	.022	.027	.031	.036	.04	.045	.05	.1	.2
197	194	202	194	209	186												
219	247	201	256	223	214												
218									204	230	217	128*					
194	197	186	204	238	239	233	210	207	144	164*	161*	156*					
						192	201	211	225	177*	162*	200*					
225										206	212	215*					
										217	191	213*					
194	189					201	208	211	189								
						173	175	203	205								
						189	182	181	217								
178			168			202											
229	209	234	224	211	202												
		222		200	201												
326															199*	313*	—
226													172*	160*	257*	167*	—
231											252		189*	199*	243*		—
288										180*	133*		143*	125*	118*		—
207													297*	179*	196*		—
													202*	234*			—
240.5	222.2	224.0	224.2	231.2	223.4	213.3	210.2	217.6	212.3	163.8	139.7	93.1	90.6	69.4	92.6	0	—ᵃ

ᵃ 15 mg. added to averages to allow for loss of weight from filter papers.

The lack of stimulation found in the starch and inulin cultures was at first attributed wholly to an occluding effect that the disperse phase of the colloidal solution might have upon the poison. The same lack of stimulation, however, was found when *Aspergillus* was grown in media contain-

TABLE 12
Sugar 3 per cent

−Zn	.0001	.0003	.0005	.001	.002	.004	.009	.018	.022	.027	.031	.036	.04	.045	.05	.1	.2
271		494	520		542												
271		471	439	458	483	576	475	88	148			120					
284	391	432	373	429	488	429	218	58	30								
220																	
327																	
262	509	532	475	460	377	499	511	214	73	46	53	13					
	474			468		382	444	155	141								
	497																
477																	
482													311	—	—	—	—
339											194	137	—				
293											25	91	82				
422	483	508	516	517	476	131	433	61	46	45							
										5							
										40							
										65							
263											23	47	26				
											28		14				
340.9	485.8	502.4	479.6	481.4	488.2	418.4	431.2	130.2	102.6	55.2	79.6	96.6	101.6	—	—	—	—ᵃ

TABLE 13
Sugar 3 per cent, Agar .25 per cent

−Zn	.0001	.0003	.0005	.001	.002	.004	.009	.018	.022	.027	.031	.036	.04	.045	.05	.1	.2
400	457	534	518	514	588	489	489	563	550	542	250*	379					
431																	
454																	
467	566	586	569	581	492	528	557	619	525	525	505	416*					
285			500		492												
345										646	528	356*					
										503	580	375*					
										604	541	540					
533															177*	200*	—
797													307*	270*	344*	437*	—
496												227*		251*	194*	418*	—
393											256	141*	178*	146*	313*		
464	496	517	518	529	525	641	558	480	225*								
	507	509	537	541	525	598	534	526*	561*								
	501	571		559	522		518	390*	494								
355													145*	128*	214*	—	
													316*	151*			
466.7	520.4	558.4	543.4	559.8	545.4	564.6	546.2	480.6	436.0	579.0	437.5	255.6	129.4	67.8	183.2	17.4	—ᵃ

ᵃ 15 mg. added to average to allow for loss of weight from filter papers.

ing very low percentages of sugar (between .25 per cent and 1 per cent). It cannot be entirely due to starvation, however; for in the case of the 3 per cent starch control and the 3 per cent sugar control, the dry weights were practically the same, yet there was a decided difference between the

appearance of the mycelia grown in solutions containing starch and zinc and the appearance of the mycelia of similar solutions with sugar as the carbohydrate. In order to separate better this starvation effect from the colloidal effect, sugar was used as the carbohydrate in varying concentrations and .25 per cent agar was added to the solutions in which the effect

TABLE 14

Starch 3 per cent

−Zn	.0003	.0005	.001	.002	.004	.009	.018	.022	.027	.031	.036
315	337	318	336	338	315	326	338				278
388		299	413	360	364	342	294	344	286		171
367		311	465	349	373	358	362	327	270		256
377		365	377	368	347		400				198
366		412	369	352	364		352				259
388		481	393	384	359		436				70
339		396	362	479	355		408				182
310		324					342	315	326	276	346
282		305					347	341	344	335	140
345		386					386	373	281	337	287
305		376					343	354	358	281	249
304		324					325	357	375	417	285
302		347					331	344	356	371	301
352.5	352.0	372.2	402.9	390.7	368.9	357.0	373.8	359.4	339.5	354.5	244.4[a]

[a] 15 mg. added to weight to allow for loss of weight from filter paper.

No correction was made for any starch that may have adhered to the filter paper when felts were reaped.

TABLE 15

Inulin 1 per cent

−Zn	.0005	.001	.002	.009	.018	.036
178						
174	200					83
181	173	184	174	213	194	
208		188	182	222	246	167
201	247					
203.4	221.7	201.0	193.0	232.5	235.0	140.0[a]

[a] 15 mg. added to weight to allow for loss of weight from filter paper.

of a colloid was to be tested. It was found that agar alone would not produce appreciable growth; so it was assumed that the agar was of little or no value as food. In each case where agar was used the control weight was a little higher, but the difference was not very great. The data secured in these tests are presented in tables 4 to 13, and are shown graphically in figure 3.

TABLE 16

Comparison of average of dry weights of mycelium of Aspergillus niger obtained with different carbohydrates in the culture medium; and of the effect on these of the presence of various fractions of a volume-normal solution of zinc sulphate.

CARBOHYDRATE	CONTR.	.0001	.0003	.0005	.001	.002	.004	.009	.018	.022	.027	.031	.036	.04	.045	.05	.1
Sugar .25%	107.0	114.0	79.0	82.0	110.0	79.0	103.5	91.5	118.5	86.5	103.5	94.4	77.8				
Sugar .25% + Agar	126.5	105.0	104.7	95.3	112.3	89.7											
Sugar .5 %	142.5		161.0	139.0		121.0	167.6	155.8	152.4	169.2	151.2	163.0	138.2				
Sugar .5 % + Agar	165.0	152.0	160.4	153.0	153.0	203.8											
Sugar 1 %	229.0	186.8	204.6	205.0	214.0	223.2	234.2	219.6	104.2	111.2	91.4	92.4	59.1	56.2			
Sugar 1 % + Agar	240.5	222.2	224.0	224.2	231.2	223.4	213.3	210.2	217.6	212.3	163.8	139.7	93.1	90.6	69.4	92.6	0
Sugar 1.5 %	198.0		302.0	319.0		343.0											
Sugar 2 %	249.0		394.0	379.0		393.0											
Sugar 3 %	340.9	485.8	502.4	479.6	481.4	488.2	418.4	431.2	130.2	102.6	55.2	79.6	96.6	101.6			
Sugar 3 % + Agar	466.7	520.4	558.4	543.4	559.8	545.4	564.6	546.2	480.6	436.0	579.0	437.5	255.6	129.4	467.8	183.2	17.4
Starch 3 %	352.5		352.0	372.2	402.9	390.7	368.9	357.0	373.8	359.4	339.5	354.5	244.4				
Inulin 1 %	203.4			221.7	201.0	193.0		232.5	235.0				140.0				

There seems to be a critical concentration of sugar which lies somewhere between 1 and 1.5 per cent. With sugar concentrations below this, no stimulation of growth was secured with zinc sulphate, either in the absence or presence of agar. With sugar concentrations above this critical concentration, pronounced stimulation of growth was obtained with zinc
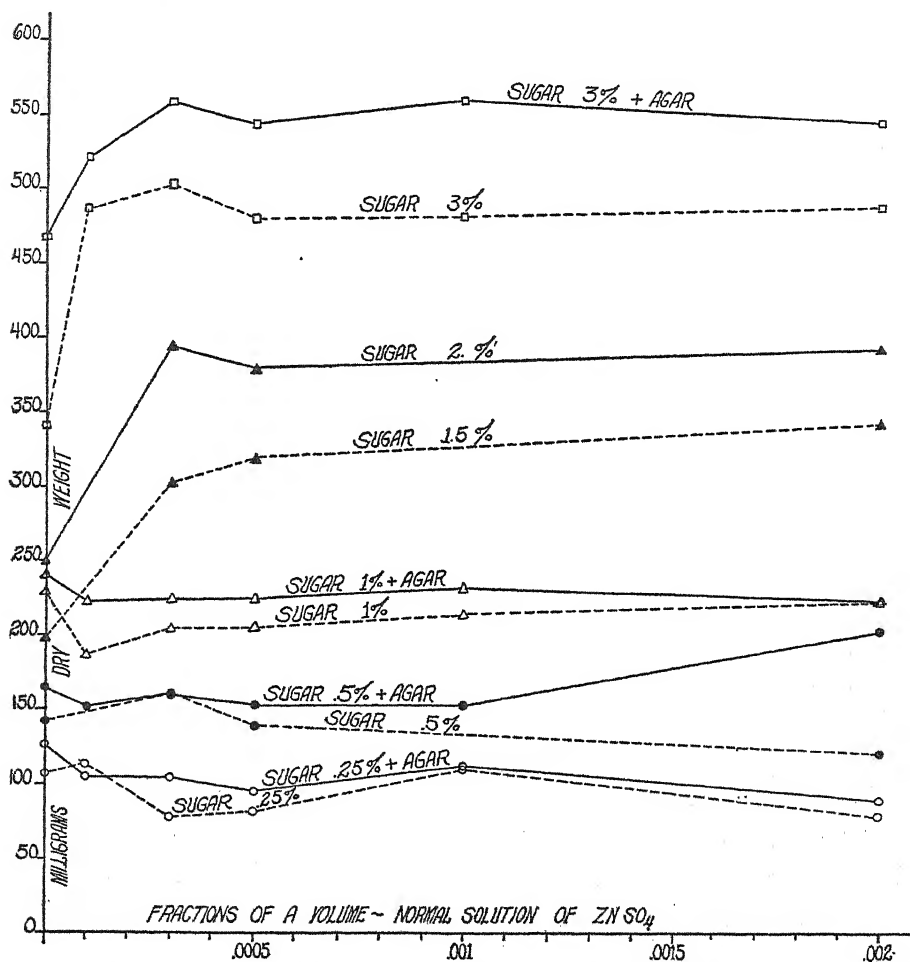
Fig. 3. Stimulation of growth of *Aspergillus niger* with ZnSO₄: nutrient solution with various concentrations of sugar, with and without agar.

sulphate in the absence of agar; in the presence of agar, some stimulation occurred, but it was much less pronounced. Thus a complete or partial lack of response to chemical stimulation may occur when the fungus is growing on a poor food supply and may be due to its lowered rates of metabolic processes, or it may occur as the result of the presence of a colloid when the fungus has a favorable food supply.

When a very low percentage of sugar was used, .25 per cent, the mycelial felts were very thin. They were smooth and produced an abundance of spores through concentrations of .002 N zinc sulphate, the highest concentration tested (tables 2 and 3). In no case was there any coloration of medium or felt. With a .0001 N zinc sulphate solution (table 4) there was a slight increase in dry weight of crop, but this amounted to only 6.5 per cent. At .0005 N the weight showed a decrease of 23.4 per cent below that of the control.

Using this same concentration of sugar with agar present, the growths looked practically the same as without agar in the medium. Even at concentrations of .036 N zinc sulphate the fruiting was as dense as in the control, and the felts were smooth. In this series, zinc sulphate seemed to have no effect as a stimulant, the control yield being the highest of any (table 5). No effect, either stimulative or poisonous, was evident until at .031 N and .036 N zinc concentrations, where the yields fell off abruptly, indicating the beginning of the toxic effect of the zinc. With as high as .027 N zinc sulphate, the decrease in weight below that of the control was only 18.1 per cent. The decrease at .0005 N was 24.7 per cent. It will be seen, then, that the response of *Aspergillus* to zinc sulphate in nutrient solutions containing .25 per cent sugar was practically the same with and without agar, with the exception of a slight increase with very low zinc concentrations without agar.

With a doubled amount of sugar present (.5 per cent) the control weight was higher (table 6). This is in accordance with the results of Haenseler (1921), who found that, as the sugar concentration was increased, the dry weights of the yield were proportionally higher. His sugar concentrations were expressed in terms of atmospheres of osmotic concentration, and he reported such an increase up to a concentration of eight atmospheres, or about 11 per cent sugar. The increase found here, with .5 per cent sugar, over the weight of the control grown with the lower carbohydrate is one of 33.2 per cent. There is, however, the same lack of response to stimulation with zinc sulphate as in the less concentrated sugar solutions. The highest amount of zinc added was a .002 N solution, but even there the fruiting was as heavy as on the control felt. In some cases, however, the zinc cultures were beginning to show slight folds. No yellow color was found in any case. The 'high-point' of stimulation for .5 per cent sugar came at the .0003 N zinc sulphate concentration, where there was an increase of only 12.9 per cent over the weight of the control, but this increase may not have been significant. The weights dropped off very gradually from there to zinc sulphate concentrations of .002 N, where the weight of the fungus was 15.1 per cent lower than the control.

Where agar was used with the .5 per cent sugar cultures (table 7), much the same thing happened as with the .25 per cent sugar and agar; that is, there resulted a decrease in crop weight, below the control. Here, however, the yield rises again to zinc concentrations of .002 N, where there is an increase of 23.5 per cent over the dry weight of the control. This increase begins with a concentration of .001 N. If significance is to be attached to this rise, it may mean that when the concentration of sugar is rather low stimulation may occur in the presence of agar, but such stimulation appears only when relatively high zinc concentrations are employed; the appearance of the cultures, however, did not suggest stimulation, and there was little difference when agar was present or absent. The fruiting of felts grown in solutions containing as much as .022 N zinc sulphate was as good as the control felts (tables 2 and 3); there was less spore production at .027 N zinc sulphate, very little at .031 N, and none at all at .036 N. Almost all cultures showed some slight evidence of stimulation, though only in the form of small folds in the felts. No yellow was found here either.

The above results for varying sugar concentrations can hardly be taken as very reliable, except in the case of the series containing .5 per cent sugar and agar, for in the others too few cultures were set up for a good average. More experiments on these series should be done before definite conclusions can be drawn.

With 1 per cent sugar, the effect of starvation amounts of carbohydrate were still very pronounced, as seen in the dry weight of mycelium produced and, to a lesser degree, in the appearance of the felts (tables 2 and 3). In no case was the fruiting as good in the zinc cultures as in the zinc-free, though there was good fruiting through concentrations of .002 N, less at .004 N, and no fruit at all at concentrations of .009 N and higher. The control felts were the only smooth ones here. Yellow color of felt or medium was not a constant point of difference between control and zinc cultures. The appearance of the fungous growth in the higher zinc series suggested that of stimulated growth such as has been reported by other workers; there was a lack of fruiting and a folding of the mycelium.

As far as the dry weights at a concentration of 1 per cent sugar are concerned (table 10), with .0001 N zinc sulphate there is a falling off in weight amounting to 18.4 per cent of the control. The reason for this is not understood. The fall in the curve (figure 3) is perhaps due to an abnormally high weight for the control culture. This is suggested by the fact that the control weight for this sugar concentration is higher than for 1.5 per cent sugar, and lies about half way between that for 1.5 per cent and that for 2 per cent sugar. Whatever the cause of the fall may be, it should be noted that a similar decrease in weight at .0001 N zinc sul-

phate occurs where there is 1 per cent sugar with agar in the medium. The dry weight increases gradually from the low point at a concentration of .0001 N to a concentration of .004 N zinc sulphate, where the maximum growth is reached. This can hardly be considered a 'high-point of stimulation', as the increase over the control is only one of 2.3 per cent.

The above results should be compared with those obtained using 1 per cent sugar with agar present. One notices at once a difference in the fruiting (table 2). Through concentrations of .009 N zinc sulphate there was as abundant spore production as in the control. At this same concentration of zinc sulphate (.009 N) without a colloid present no spores were formed at all. With agar present, on the other hand, there was still some spore production, less than the control, to be sure, with .018 N, .022 N, and .027 N concentrations of zinc sulphate; and production of spores did not cease entirely until a strength of .031 N was reached. The presence of a yellow color of felt or medium was again variable. In all cases except the control there was very slight stimulation in the form of small folds in the felts (table 3).

The average weight of the control grown with agar present was very slightly higher than that grown in 1 per cent sugar with no agar (table 11). Except for a slight drop with .0001 N zinc sulphate, the weights at increasing concentrations of zinc sulphate remained practically the same, up through a concentration of .022 N. At no point, however, did the weight of zinc cultures come up to that of the zinc-free cultures.

Using 1.5 per cent sugar in the nutrient solution, the starvation effect on the response of *Aspergillus niger* to the presence of zinc sulphate seemed to stop suddenly. With small amounts of zinc present there was a considerably increased growth which begins to be comparable to that found by Richards and others with a higher sugar concentration. Only a few series were set up with the nutrient containing 1.5 per cent and 2 per cent sugar, and none with agar present at these two concentrations. In each case, also, .002 N was the highest amount of zinc sulphate used. The fruiting in these series was affected by the zinc (table 2); for in the nutrient with 1.5 per cent sugar, there was some fruit where zinc sulphate was present in a concentration of .0003 N, and a very little where .0005 N and .002 N concentrations were present. In the nutrient with 2 per cent sugar there was only a very little fruiting in any zinc cultures. With both 1.5 per cent and 2 per cent sugar all but the control were yellowish and showed signs of folding of the felts (table 3).

With 1.5 per cent sugar the average weight of the felts was considerably higher when zinc was present (table 8), there being an increase of 73.2 per cent over the weight of the control at the high point, .002 N. (This was the highest concentration of zinc sulphate tested.)

The control of the 2 per cent sugar series was about 50 mg. heavier than that of the 1.5 per cent sugar solution (table 9). The weights of the 2 per cent sugar solution followed those of the less concentrated quite closely, except that the high point was at a zinc content of .0003 N. The increase in weight over the control at this point was one of 58.2 per cent.

With 3 per cent sugar the evidences of stimulation, as far as gross appearance is concerned, were even more pronounced (tables 2 and 3). With the exception of the concentrations of .0001 N where there was a very little, the zinc cultures showed no fruiting at all. Here, too, the yellow coloration was not constant. Stimulated felts, like those described by Richards, appeared in all zinc cultures; that is, mycelium showing a lack of fruiting, and tough leathery, much folded vegetative growth.

The dry weights, too, showed this stimulation (table 12), there being an increase of 47.4 per cent over the weight of the control at a .0003 N zinc content, the high point for the series. From here on, the weights decreased gradually with higher amounts of zinc. By comparing the graphs of the dry weight of fungus grown with increasing amounts of zinc in nutrient containing 3 per cent, 2 per cent, and 1.5 per cent sugar solutions (figure 3) it will be seen that they are all very much the same, each higher sugar percentage giving correspondingly higher weights throughout the series.

Where agar is present with the 3 per cent sugar in the nutrient solution, there is some evidence of a reduced response to zinc sulphate (tables 2 and 3). There was a slight amount of fruiting where zinc was present in a .004 N and lower solution. Evidences of stimulation were seen in all the solutions containing zinc, as far as folding of the felt was concerned. In no case, when agar was present, were the felts as tough and leathery in consistency as when only sugar was used in the medium. The presence of yellow here, too, was not constant.

The weights of fungus grown in 3 per cent sugar and agar (table 13) corresponded quite closely to those of the 3 per cent sugar solutions alone, when lower concentrations of zinc sulphate were used. The control weight was considerably higher than when 3 per cent sugar alone was supplied the fungus, but the reaction to zinc was not so pronounced with agar present in the solution. It may be, then, that the control was somewhat stimulated to begin with; but this hardly seems probable, for the macroscopic appearance of the controls in all cases was of a smooth, densely fruiting mycelium. The maximum weight for this series was obtained with a zinc concentration of .027 N, where the increase over the control was 24.1 per cent. At .0003 N, the high point of stimulation for 3 per cent sugar alone, there was, with agar present, an increase of only 19.6 per cent in dry weight, as compared with an increase of 47.4 per cent for sugar alone.

In addition to the inhibiting effect of colloids on the stimulating action of zinc sulphate, it was observed that when a colloid was present in the nutrient solution much greater quantities of the poison could be tolerated by *Aspergillus* than when no colloid was present. Special attention was paid to this, and to the lethal amounts of zinc for nutrients containing
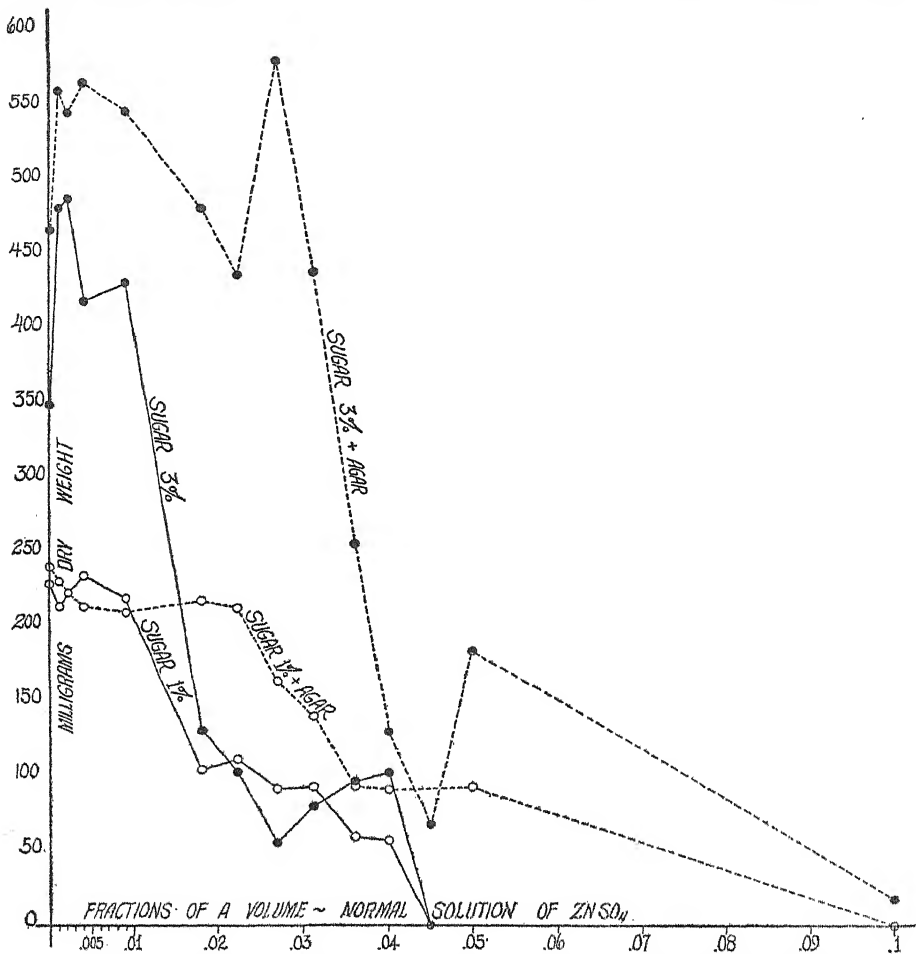
Fig. 4. Effect of agar upon the toxicity of ZnSO₄ for *Aspergillus niger*.

1 per cent and 3 per cent sugar, with and without agar. The data for this are shown graphically in figure 4.

With 1 per cent sugar solutions (table 10), the weight of fungus began to fall off from the high point, .004 N zinc sulphate. The loss in weight up to a concentration of .009 N zinc sulphate was very gradual, but from there on there was a definite decrease to some point between .04 N and

.045 N solutions, where there was no growth at all. The poisonous effect of the zinc began to be shown very definitely at .009 N concentrations where the felts were no longer complete, and the growth appeared in scattered patches. These scattered bits of growth were in some cases on the surface, in others, submerged. Between concentrations of .018 N and .045 N zinc sulphate there was still a decrease in mycelium weight but it was very gradual.

A striking difference is shown between the weights of mycelium using 1 per cent sugar nutrient and those where agar was also present (table 11). At a zinc sulphate concentration as high as .022 N the weight decreased only 11.7 per cent below that of the control, and only 8.2 per cent below that of a .001 N concentration. (It will be remembered that in these series the control weight was higher than any of the zinc culture weights, the next highest point being with a .001 N zinc sulphate solution.) The poisonous effect of the zinc here, as far as the completeness of the mycelial growth is concerned, did not begin until a concentration of .027 N was reached. From .022 N concentrations of the poison on, there was a steady, although gradual, decrease in weight of crop. At .045 N zinc sulphate, there was no longer any growth of *Aspergillus* with no colloid present; but when there was a colloid present there was some growth in two cases out of five even at a concentration of .1 N zinc sulphate. The average for the series was zero for this concentration, which may therefore be considered as lethal. Thus, with over twice as much zinc in the solution, when a colloid was present, *Aspergillus* was still able to grow.

The same reduction of the toxicity of the zinc salt held for 3 per cent sugar nutrient solutions containing agar. With no agar present there was a gradual decrease in weight from the high-point, .0003 N (table 12). The falling off was rather more abrupt between concentrations of .009 N and .018 N than was that for 1 per cent sugar alone, which may indicate that there was a starvation effect that influenced the poisonous action of zinc sulphate as well as its stimulative action. The same lethal point was found, however, for the 3 per cent sugar. Though the weight was considerably higher for 3 per cent than 1 per cent sugar cultures at .04 N concentrations of zinc sulphate, there was no growth at all at concentrations of .045 N. In this series the felts were first incomplete at zinc contents of .004 N, whereas with 1 per cent sugar this was not until .009 N in one case, and .018 N in three cases. This, too, seems to indicate the possibility of a 'starvation' effect which influenced the toxicity as well as the stimulating power of the zinc.

With the higher sugar content and agar (table 13) the felts were complete in some cases only until .018 N zinc concentrations were reached, but

the majority were complete up to concentrations of .036 N. The decrease in crop weight was gradual, beginning at the .004 N zinc sulphate solution, the high point for this series. The sudden increase in weight at .027 N zinc sulphate concentrations here seems rather abnormal. This might be explained on the ground that the agar which was in the medium may have been weighed with the felts, and notes not taken of it at the time, so that the higher weight may be due, at least in part, to dried agar. Whereas, with 3 per cent sugar alone, growth stopped at zinc concentrations between .04 N and .045 N, when agar was present there was still some slight growth at .1 N. The lethal point here, then, lay somewhere between .1 N and .2 N concentrations of zinc sulphate.

DISCUSSION OF RESULTS

Richards (1897) attempted to determine the effect of varying amounts of iron, zinc, cobalt, nickel, manganese, lithium, aluminium, and silicon salts and some organic substances, such as cocaine, morphine, amygdalin, antipyrin, and chloral hydrate on the growth of *Aspergillus niger*. He varied the nitrogen rather more than the carbohydrate source. Some series were set up, however, using glycerine with different nitrogen sources, and one substituting sodium acetate for sugar. His cultures were grown at 30°.

In all cases, Richards considered that abundant food was present. Glycerine, as a carbohydrate source gave a normal growth, he found, the conidia ripening, if anything, a little earlier than in sugar nutrient cultures. He did find, however, that on a poorer food substance, or by the addition of glycerine, though the mycelium developed more slowly, the rate of increase of growth due to the presence of zinc was almost the same as on a good food. His tables show an increase over the control of 155.3 per cent at the high-point (.0003 N zinc sulphate) in one series, and of 85.7 per cent at the high-point (.004 N zinc sulphate) in another. In two cases out of three, then, he found the proportional increase with zinc to be the same for sugar and glycerine nutrient solutions; in the other case, it was somewhat higher for the sugar solutions.

Watterson (1904) likewise reported that, though she got lower yields with glycerine as carbohydrate, the fungus responded with a decided increase in weight to the presence of zinc in the solution. Her figures show an increase of 144.3 per cent in one case, and of 102 per cent in another of dry weight of yield at a zinc concentration of .0005 N. Glycerine, therefore, though it appears to be a poorer food than 5 per cent sugar, cannot be compared to as low a sugar concentration even as 3 per cent.

The above results are contrary to those found in this work when very

low percentages of sugar were used. It does not seem possible, either, that stimulation would finally result in these 'starvation' cultures, for after four days there was an abundance of spores present with even the highest concentrations of zinc in the medium.

Asparagin in the medium, as a nitrogen source, according to Richards (1897), also did not affect the action of the zinc. He used another poor food stuff, sodium acetate. The growth here was slow, but there was nevertheless an increase with concentrations of .0003 N zinc sulphate of 83.3 per cent that of the control. The weights were very low here, a maximum of 55 mg. being obtained for this series. These results, then, do not agree with those obtained in this work with sugar percentages which yield as low a growth.

An explanation for the lack of response to zinc in those cultures where very low percentages of sugar were used is probably to be found in the greatly reduced vitality which must accompany growth on such a poor substratum. That this does not hold for spore production is evident from the very heavy fruiting obtained for all the cultures, with and without zinc, using sugar concentrations of .25 per cent and .5 per cent. This seems to be contrary to the view expressed by Richards (1910) that the ' . . . spore-forming process is one demanding a greater expenditure of energy than the mere vegetative growth of the hyphae.' On the other hand, deficiency of food, according to Pfeffer (1900) often induces the formation of spores. He also says, however, that if plants are too much starved, or growth almost suppressed by alkalis, acids, or poisons, the production of reproductive bodies almost or entirely ceases. Frank (1895), also, reported that with a lack of sufficient food, both the growth and fruiting of plants are below normal. Kiesel (1912) tested the effect of various acids on the germination of spores, the development of mycelium, and the production of spores. He concluded that all the acids tested had the same order as to potence for all three, so that one acid reducing the vegetative growth more than another should also reduce the formation of conidia more than the other.

It may be that with low sugar concentrations, mainly the toxic effects of the zinc show, as in those series where the control is the high point, or nearly the high point. This reaction to poor food supply may also account for the rather lower percentage increase due to the stimulative effect of zinc, obtained in this work for 3 per cent sugar, than has been found to occur by other workers who used mainly 5 per cent sugar. The vitality of the fungus when starved may be so low that it has not enough energy to show a response to the stimulant. Perhaps, when it is starved, the fungus can be said to have reached its greatest growth activity for the amount

of sugar present. In that case, the results obtained here might be compared to some obtained by Richards (1897) at quite the other extreme. When he had added iron to the medium in quantities which gave greatest growth for *Aspergillus niger*, he then found that no further increase in yield could be brought on by the addition of zinc sulphate. This he explained by saying that after the mycelium had reached the maximum of its growth activity, it could react to no more stimulation.

According to Richards (1910), 'The condition of the stimulated plant itself may cause a variation in the optimum concentration of the stimulant, as is shown by the effect of rise in temperature on the lowering of the toxic or stimulatory dose.' Here, it seems to me, we are unquestionably dealing with a peculiar condition of the fungus, brought about by insufficient food-supply.

Pfeffer (1900) states that ' . . . starvation may cause the reassimilation of metabolic products which under normal conditions remain permanently withdrawn from metabolism.' He also says that where a plant is stimulated by chemical elements 'increased growth appears to be due to a general power of reacting against injurious influences possessed by living organisms.' This power seems, paradoxically, from the results here obtained, to be increased, the weaker the condition of the fungus. He also says, in another place, that although deficiency of food diminishes the activity of growth and of respiration, it may cause the plant to work more economically.

Terroine, Trautmann, and Bonnet (1925) concluded that the metabolism of the cell is not modified by the concentration of food available. They measured the yield of energy produced (proportion of weight of crop to sugar used) and found that the concentration of nutrient elements might vary in the proportion of 1–15, and the utilization of energy for growth would remain the same. They grew *Sterigmatocystis nigra* (*Aspergillus niger*) in glucose solutions of 2 per cent, 10 per cent, 20 per cent, and 30 per cent. Zinc sulphate was present in all cases as a part of the culture medium.

Richards (1899) found that the economic coefficient of sugar was raised by the addition of zinc sulphate; in other words, there was a larger crop for a given amount of sugar when zinc was present in the solution. It would be interesting to determine what the result of a very poor food supply is on the economic coefficient of the sugar. According to Richards, one reason for the increased growth of the stimulated felts is the increased availability of the sugar. Why the zinc should not increase the availability of small amounts of sugar as well as of larger seems rather difficult to decide.

Pfeffer (1900) placed grape and cane sugar at the head of the list of carbohydrates of varying nutritive value for *Aspergillus niger* and *Penicillium glaucum* with ammonium nitrate as nitrogen source. He made the comment, however, that the nutritive value can be changed by temperature or concentration of the nutrient solution. The latter seems to be the case here, the change being, however, in the concentration of the sugar itself. According to him, 2–15 per cent grape or cane sugar makes a favorable medium for growth.

Aside from the results obtained using very low percentages of sugar, there is the question of the lack of response to zinc shown by the fungus when a colloidal solution was present in the medium. That this phenomenon is due to the colloidal nature of the substratum seems likely, because there was the same lack of stimulation shown with starch, a good energy source for *Aspergillus*, inulin, which also seems to be good as an energy source, and agar, which alone is a very poor food, but which inhibits response to zinc when present in the solution with sugar. It seems logical to account for this lack of response by assuming that the zinc in the solution is adsorbed by the disperse phase of the colloidal particles present.

This selective adsorption by colloids is a common enough occurrence. Hatschek (1916) in his *Introduction to the Physics and Chemistry of Colloids*, says: ' . . . various substances may not be adsorbed to the same extent, . . . or one or the other may be removed selectively, as, e.g., the coloring matter from sugar solutions.' In the case of charcoal and metallic salts in an aqueous solution, according to Taylor (1915), (in what he considers a pseudo-adsorption phenomenon) 'some salts of heavy metals are so completely removed from solution by it that not a trace of the metal can be detected in the liquid . . . but what has been taken out by the charcoal cannot be removed from it by washing with water.' No attempt was made here, to be sure, to find out whether any zinc was left in the solutions which had colloids present, or whether the starch, inulin, or agar had taken up the zinc. Taylor also says that in such cases the liquid then becomes strongly acid. If it were merely increased acidity which is responsible for stimulation, then, as Steinberg (1919) suggests, we should have greater instead of the same growth with a colloid present, due to this increased acidity of the medium. In the case of this work, no attempt was made to determine the acidity before or after the fungus had been growing in the medium.

That starch, too, removes substances from solution is reported by Lloyd (1911). To be sure, his results apply to various kinds of starches in the cold, but it would seem that they would also apply to the starch when 'dissolved.' He considers the loss of a neutral salt, like potassium

chloride, from solution, to be caused by adsorption of it by the starch.

Inorganic salts, acids, and bases are feebly adsorbed from water according to Taylor, but Carey (1923) has shown that an increase in acid concentration causes an increase in weight of acid adsorbed per gram of substance. This might hold good for adsorption of the metallic ion also from an acid solution. The culture medium is decidedly acid, and would be increasingly so the more zinc sulphate is added.

Long (1915) found that, with *Opuntia Blakeana* in a nutrient solution, there was practically always a slightly increased swelling over that in distilled water. His medium was neutral to begin with, but he does not say whether it remained neutral after the cactus had been in it.

The only reference to a similar inhibition of the poisonous effect of dissolved salts on plant tissues found was in a paper of Kahlenberg and True (1896). These workers were concerned with the poisonous effect of dissolved salts on roots of *Lupinus albus*. They attributed the lack of response to the poison to the lower toxicity of complex ions formed, though in each case the 'complex ions' might have been colloidal solutions. When copper salts were used, they concluded that the 'copper ion is more poisonous than a complex ion which contains copper.' Using dialyzed ferric chloride, which they said, contained no ferric or chloride ions, they found that the 'complex ions containing ferric iron in the dialyzed iron solution' were more poisonous than ferric ions of ferric chloride. The possibility of the effect being due to a colloid seems even more striking from their next results. They say that if dextrine is added first to a solution of mercuric chloride, precipitation of mercuric oxide by potassium hydroxide is prevented, so no mercuric ions are present. This solution is less poisonous than mercuric ions alone. They explain this on the ground that 'mercury has united with the dextrine to form a complex ion.' Is it not possible, however, that the colloidal dextrine adsorbs the mercuric ions from the solution? Their conclusion is: 'If the addition of certain substances to a solution containing a physiologically active ion forms a complex ion of much less powerful action, it follows that these additional ingredients afford a means of reducing, so to speak, the physiological action of the simple ion.' It would seem to me that the same conclusion could be drawn from the presence of colloids. Czapek (1913), in reviewing this paper, refers to the above effects as due to their colloidal nature, not mentioning the 'complex ion.' Pfeffer (1900) says in this connection, that ' . . . the presence of other substances may cause a soluble poison to be precipitated, or converted into an innocuous compound.'

The question of changes in permeability of the cell membrane due to the presence of a colloid, rather than the adsorption of the metallic ion by

the colloid might come into play here. Donnan and Harris (1911) have shown that when congo-red, a partial electrolyte, is present on one side of a parchment membrane, sodium chloride does not distribute itself in equal concentrations on both sides. In the opinion of Richards (1910), however, the different amounts of a substance necessary to produce stimulation is a question more of specific differences in the protoplasm itself, than of the permeability of the cell membranes.

On the whole, it seems to me that the adsorption by the colloid of the poison present is the best explanation for lack of response by *Aspergillus* under such circumstances to zinc sulphate. This might explain the fact that for years experimenters have been growing *Aspergillus niger* on slices of bread, far from 'physiologically clean,' and getting normal growth, although in order to get an 'unstimulated' growth in culture flasks, it is necessary to use purest chemicals and double-distilled water, and to have all culture flasks 'physiologically clean.'

The difference in lethal dose with and without a colloid present also seems an indication that the colloid can take up at least some of the zinc in the solution, if not all of it. Whether more agar in the solution would remove still more poison, and thus allow the fungus to grow at still higher zinc sulphate concentrations was not tested in this work. Since the amount of adsorption depends on the surface of the colloidal particles, this might be expected to be the case, at least for limited amounts. Depending on how the experiments were to be carried out; that is, were one to increase the amount of zinc sulphate rather than of agar, other factors would have to be considered, such as increased turgor pressure and acidity.

Richards (1897) found that *Aspergillus niger* was more susceptible to zinc than to any of the other metals he used. In a later paper (1899) he considered solutions of .002 N zinc sulphate concentration as just 'within the range of the toxic effect.' At this point the average weight of mycelium had dropped almost to the weight of the control felts. The economic coefficient of sugar also had fallen almost to that of the control. According to Kunkel (1913), zinc nitrate was the most toxic for *Monilia sitophila* of all the nitrates tested. In .000034 M solutions it completely inhibited the germination of spores when the fungus was grown in 5 per cent starch solutions. Latham (1905) found that chloroform behaved like heavy metals, causing stimulation in small quantities, and a cessation of growth in larger quantities. She found that germination was permanently stopped when concentrations of over 1 cc. per liter were used. With asparagine instead of ammonium nitrate in the nutrient, the sensitivity of *Aspergillus* to the poison was increased, development being prevented at concentrations of .67 cc. of chloroform per liter of solution. Kunkel (1913),

on the other hand, reported that when peptone was added to his starch media, the toxicity of ferric nitrate to *Monilia sitophila* was lessened.

From the series reported here with 1 per cent and 3 per cent sugar and no agar in the medium, it is forcibly brought out how resistant *Aspergillus niger* is to zinc sulphate in large quantities.

SUMMARY

A colloidal substratum inhibited the increased vegetative growth of *Aspergillus niger* usually found resulting from the addition of small amounts of zinc sulphate to the medium. A similar lack of stimulation also resulted when the carbohydrate source was present in low concentrations. The presence of a colloid in the nutrient solution also had an inhibiting effect upon the lethal doses of zinc sulphate for *Aspergillus niger*.

The above work was done in the Botanical Laboratory of Barnard College, Columbia University, under the direction of the late Professor Herbert M. Richards. The writer greatly appreciates his advice and interest.

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Chlorotylites, a fossil green alga from Alabama

MARSHALL A. HOWE

(WITH PLATE 15)

In November, 1931, Dean Edward W. Berry of The Johns Hopkins University, at Baltimore, sent to the writer a siliceous fossil from Alabama, together with a ground section thereof, in the belief that it represented an alga. A second specimen from the same locality was forwarded later, with the information that no more material was available, that both specimens had come from the Alabama Geological Survey, that the collection was made many years ago, and that name of collector and date of collection were unknown. It was further stated that the specimens came from Black Bluff on the Tombigbee River in Sumter County and from the Sucarnoche formation of the Middle Midway and that their general age was Lower Eocene. Professor Berry added, "Marine fossils are found in the outcrop, but there is also a bed of lignite near the top of the Bluff, which is obviously non-marine." Study of the fossils convinced the writer that organism was closely related to the recent genus *Chlorotylium*, the representatives of which inhabit fresh water and are found, for the most part, in rapidly flowing streams. They appear to be widely distributed, but are collected rather infrequently, presumably because they are normally heavily coated with lime and form small crusts that the average botanist passes by as something foreign to his field. Descriptions of genus and species follow:

Chlorotylites M. A. Howe, gen. nov.[1]
Class Chlorophyceae, family Chaetophoraceae. Thallus discoid, calcareous (or siliceous by replacement), consisting of compacted dichotomously branched fastigiate filaments, these composed of uniseriate cells of variable length, two

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[1] *Chlorotylites* gen. nov. (fam. Chaetophoracearum, class. Chlorophycearum) Thallus discoideus, calcareus (aut denique siliceus) e filis compactis dichotomis fastigiatis e cellulis uniseriatis in longitudine variabilibus, duobus aut tribus brevioribus cum una aut pluribus longioribus saepe alternantibus, compositus. Alga fossilis eocenica *Chlorotylio* Kuetz. recenti affinis.

Chlorotylites Berryi sp. nov. Thallo libero, disciformi (circ. 2½ cm. diam., 1 cm. crasso) in sectione lacunas paucas et lobos et convolutiones cerebriformes anastomosantes in verrucas aut mammillas stipatas superficiales 0.5–2 mm. latas apicibus erosis et lamellatis, desinentes monstrante; filis 8–13μ latis, cellulis 0.5–3-plo longioribus.

In loco "Black Bluff" dicto, in comitate "Sumter," Alabamae, Am.-Bor., in stratis geologicis inferiori-eocenicis.

or three shorter cells often alternating with one or more longer ones. Lower Eocene fossil, similar to recent *Chlorotylium* Kütz. in structure, but apparently unattached and more radial or discoid in mode of growth, with less regular development of long and short cells and less obvious lamellation. Type species, *Chlorotylites Berryi*.

Chlorotylites Berryi M. A. Howe, sp. nov. Thallus free, disciform (in the two specimens seen about 2 ½–5 cm. in diameter and 1 cm. thick) showing in section occasional lacunae and anastomosing cerebriform lobes and convolutions, ending in crowded superficial verrucae or mammillae mostly 0.5–2 mm. broad, the exposed apices often worn and lamellate; filaments 8–13μ broad, the cells mostly 0.5–3 times as long.

From Black Bluff, on Tombigbee River, Sumter Co., Alabama—Lower Eocene. Type specimen and section in the Herbarium of The New York Botanical Garden.

The species of the recent genus *Chlorotylium* form calcareous, often confluent hemispheric cushions on rocks, stones, wood, or leaves in freshwater ponds and streams, usually in rapidly flowing water. The specific name in *C. cataractarum*, the type and best-known species of the genus, sufficiently indicates its ordinary habitat. Of *Chlorotylites Berryi*, we have seen only two specimens. In the smaller one, of which our only ground section was made, the two faces of the disc are developed about equally; one could hardly say which was the upper surface and which the lower, but in the lower specimen there is a manifest differentiation of the two faces, the larger or shaded surface showing smaller and browner verrucae. The smaller pebble was apparently turned over frequently by the water-currents, so that it had no opportunity to develop dorsi-ventrality, while the larger heavier pebble was less often overturned. The one section made shows no trace of any original matrix on which the alga began its growth. This matrix was probably a leaf, a supposition that seems to explain both its disappearance and the flattened form of existing fossil. The fossil as found is siliceous, but it seems fair to assume that the original organism was calcareous, like its modern close relative.

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Explanation of plate 15

Chlorotylites Berryi

1. Photograph of the two specimens, natural size. The one at the right is the type.
2. A transverse ground section, enlarged somewhat less than two diameters (19/11).
3. A portion of the above section, showing the general surface at top, ×51.
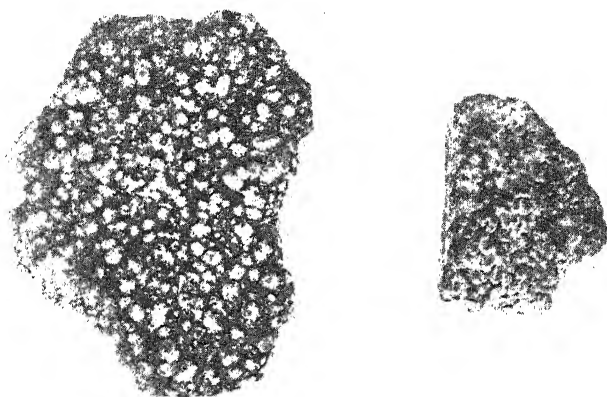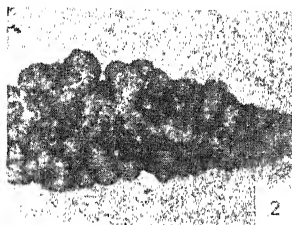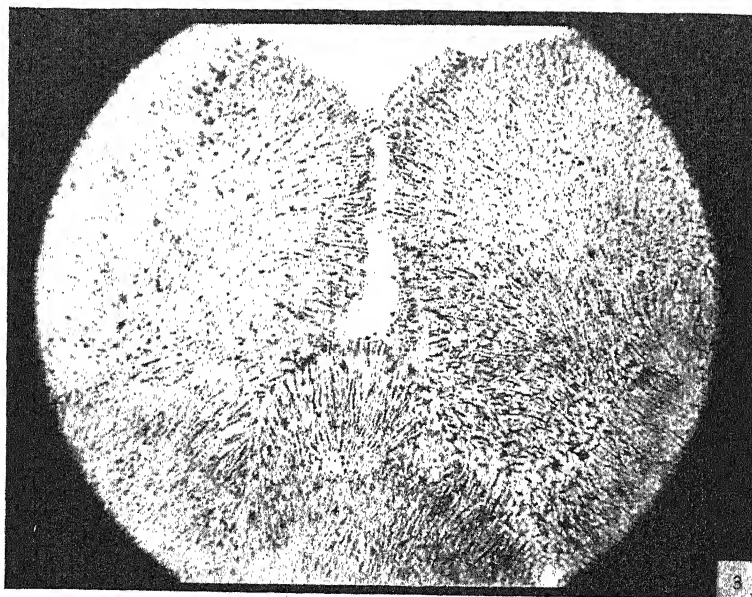
A new ascocarpic species of Penicillium

MARJORIE E. SWIFT

(WITH A TEXT FIGURE)

The difficulties of understanding the natural relationships of species of fungi which have the penicillus type of asexual fructification and their relation to other ascomycetes are largely due to the rarity with which the perfect stages are produced in nature or in culture. It is well known that in other groups of ascomycetes similar types of asexual fructifications are sometimes connected with ascocarpic forms belonging to widely separated genera. Until some way is found to induce the formation of perithecia by the different types of *Penicillium*, their true relationships must remain a matter of conjecture. When, therefore, a species which forms ascocarps readily in culture is found, it becomes a subject of considerable interest to mycologists.

An unusual species recently appeared in our laboratory. It was one of three fungi isolated from a water-soaked spot on a Begonia leaf. It produces both the ascocarpic and conidial stages in culture, and its characters seem to be such as to warrant its being described as a new species.

Penicillium bacillosporum sp. nov.

Mycelio funiculoso, in variis substratis varie colorato, e.g., coloris pallide albulo-flavi in agaro maidis, coloris pallide rubidi in agaro dextroso. Substratis quoque coloratis, agaro maidis viridi, agaro dextroso rubro.

Conidiis 3–6×1–1.5μ, bacilliformibus, non numerosis; penicillo plerumque monoverticillato, sed interdum biverticillato; sterigmatibus 10–15×2.5–3.5μ; conidiophoris brevibus, 25–50×3–5μ; peritheciis 137–150μ, sub-albis vel albo-flavis; ascis 10–12.5×7.5–10μ, globosis; ovoideis vel piriformibus, octosporis; sporidiis 3.5–4μ, globosis, tenuiter verrucosis.

Mycelium funiculose showing marked color differences on different nutrients, from pale yellow on corn meal agar to salmon on dextrose agar. Chromogenic effects in the medium itself also varied from bright green in corn meal agar to red in dextrose agar.[8]

Conidia 3–6×1.5μ, bacillar, not numerous, in long diverging thread-like chains, persistent at first, fragmenting in age. Penicillus predominantly monoverticillate, but occasionally biverticillate. Sterigmata 10–15×2.5–3.5μ, five or six in a whorl. Conidiophores short, 25–50×3–5μ, branched, formed mostly at right angles to the trailing sometimes funiculose hyphae.

Perithecia averaging 137–150μ in diameter, usually whitish to pale yellow, with thin but definite wall of interlacing hyphae. Asci 10–12.5×7.5–

10μ, globose, oval or pear-shaped, 8-spored. Ascospores 3.5–4μ, globose, finely verrucose, hyaline to yellowish in age.

On Begonia leaf, probably saprophytic.

Type locality, New York City.

Type culture and slide preparation deposited in the Herbarium of The New York Botanical Garden.

POSITION IN THOM'S GROUPS

According to Thom (1930), practically the only Penicillia which are known to produce ascocarps with any regularity belong to the *P. luteum-purpurogenum* group. Those reported in other groups are either doubtfully identified and described or have been found but once. No one except Schwartz (1927), for example, has ever been able to induce the sclerotia of *P. italicum* to develop asci; the ascocarp of *P. glaucum* described in detail by Brefeld (1874) has never been reported since, and, according to Thom (1930, p. 561), may have belonged to an *Aspergillus*. The strain of *P. candidum* described by Morini (1888) as producing perithecia has not been found again.

The characters of the *P. luteum-purpurogenum* group (Thom, 1915) in which the most common ascocarp-producing species fall are (1) a biverticillate type of conidial apparatus, (2) yellow color associated with aerial growth, and (3) yellow to red coloration in the medium. *P. bacillosporum* has a predominantly monoverticillate penicillus, although biverticillate individuals are occasionally found. The color of the aerial growth varies on different media from very pale yellow to bright salmon. The chromogenic effects in the medium range strikingly from bright clear green in corn meal agar to red in dextrose agar medium. The types of ascocarps and ascospores in the *P. luteum-purpurogenum* division, judging from descriptions, vary sufficiently to admit this species. The perithecium wall in this group ranges from the loosely constructed, easily crushed mass of hyphae typical of *P. Wortmanni* to the peridium of thick cells of *P. avellaneum* described by Thom and Turesson (1915), and the three-layer brittle wall of Lehman's (1920) *P. spiculisporum*. The perithecium of our *Penicillium* is easily crushed like that of *P. Wortmanni*, but its wall shows two rather distinct layers of compactly interwoven cells. The ascospores of the *P. luteum-purpurogenum* group range from the tricostate type of *P. luteum* to the echinulate and pitted types of *P. Wortmanni* and *P. avellaneum*. *P. bacillosporum* has ascospores with finely verrucose protuberances appearing as minute spines except under very high magnification where their wart-like form can be detected.

In view of these similarities and dissimilarities, the question as to whether or not *P. bacillosporum* belongs in the *P. luteum-purpurogenum*

group must be left open until further data on the ascocarp-forming species have made their classification more logical. Dr. Charles Thom, however, has examined cultures of this fungus and, despite the predominance of the monoverticillate conidial apparatus, states in a recent letter that he believes the shape of the sterigmata justifies its being placed "in the group specified by *P. spiculisporum* of Lehman" from which it "is properly separated by the conidium formation and the shape of the ascospores."

There are several characteristics of *P. bacillosporum* which make it distinctive as a species. The conidium is almost rod-shaped, with its length often as much as five times its width. These spores are produced very scantily on most media.[1] They can best be observed by examining a corn meal agar plate culture under low power. They occur in long thread-like diverging chains which break up in an angular fashion somewhat like chains of rectangular oidia. A second noticeable characteristic is the very prompt appearance on a variety of media of abundant, very pale yellowish perithecia, particularly marked on corn meal agar. Macroscopically the contrasting chromogenic effects produced in different media, to be described later, also mark the fungus as unusual.

SEXUALITY

Single spore culture work, with both conidia and ascospores, has shown *P. bacillosporum* to be homothallic. Twenty-seven single conidia and ten single ascospores were isolated and grown. Ascocarps appeared on corn meal agar within three days after a single spore of either type had been sown, provided the cultures were kept constantly at 28° C. Mature ascospores began to appear after twelve days.

Among the ascocarp-forming species of *Penicillium* studied to date the homothallic type seems to predominate. Schwartz (1927) concluded that *P. italicum* was homothallic after sclerotial bodies developed in cultures from single ascospores, these sclerotia being apparently identical with those from which he had obtained the ascospores by special treatment. Lehman (1920) does not state that he obtained ascospores from monospore cultures of *P. spiculisporum*. However, cultures from single spores of a strain of his species have been grown in this laboratory and they have produced ascocarps abundantly. *P. Wortmanni* and three undescribed species have also been tested for their sexuality and all produce ascocarps from single conidia as well as single ascospores.

[1] The terms "scanty" and "not abundant" in describing conidial production are used to contrast *P. bacillosporum* with the common imperfect forms of the Penicillia which produce spores in conspicuous powdery masses. The conidia are present, however, in numbers quite sufficient for diagnostic purposes.

The only case of heterothallism in the Penicillia thus far claimed to have been demonstrated was that of *P. luteum* (Zukal) Wehmer, reported by Derx (1926). He found that no ascocarps were formed in single spore cultures, but when certain cultures were paired fruit bodies developed. The possibility of other such cases is suggested by the fact that some ascogenous species have been said to lose their ability to form ascocarps after a period of culturing. The dying out or the accidental elimination of one of the unisexual strains might account for such an occurrence. Moreover, the abundance of "imperfect" species makes it feasible to suppose that these are unisexual strains which, if paired in the proper combinations, might produce their perithecial stage.

<div align="center">MORPHOLOGY</div>

Conidia (fig. 1, a) occur in comparatively small numbers on most media. Their long divaricate tangled thread-like chains break up readily in old cultures, but are quite persistent when young, at which time the individual spore limits are often barely discernible. The spores are rod-like in form, $3–6 \times 1–1.5\mu$, becoming slightly larger at one end with maturity, and in very old cultures approaching an oval contour. The terminal spore of the chain is consistently shorter than the others and nearly oval. Upon germination the spore swells to approximately twice its width, but not increasing appreciably in length, and sends out one or two germ tubes which quickly begin to septate and branch. The appearance of the young colony differs greatly on different media. On corn meal agar the mycelium is almost entirely submerged and hyaline until the very pale yellow ascocarps begin to appear (after three days) at which time the rather scattered conidial branches also develop on trailing, sometimes funiculose, hyphae, and the green color begins to appear in the medium.

The sterigmata occur usually in one verticil, five or six in the whorl (fig. 1, a). They are usually acuminate to lanceolate, with their form varying, however, depending upon age and fertility. One short side branch frequently occurs, suggesting a biverticillate condition, or two or three shorter branches may form a true verticil of metulae. This definitely biverticillate penicillus, however, is not common.

The conidiophores are short, usually extending at right angles from the main hyphae. Branching of the fertile hyphae is common. The walls of the conidiophore sometimes show a slight roughening.

Ascocarps are approximately globose, non-ostiolate, averaging 137–150μ in diameter, and surrounded by a loose mat of branching roughened hyphae usually very pale yellowish. This weft of mycelium causes considerable difficulty in cytological study by enclosing the fruit body in a

film of air which prevents good fixation. The wall of the perithecium (fig. 1, e) is composed of interlacing, quite closely compacted, hyphae in two more or less distinct layers, the outer about 5–7.5µ thick, darkly-staining, and merging gradually into the inner which is composed of more lightly-staining larger cells.
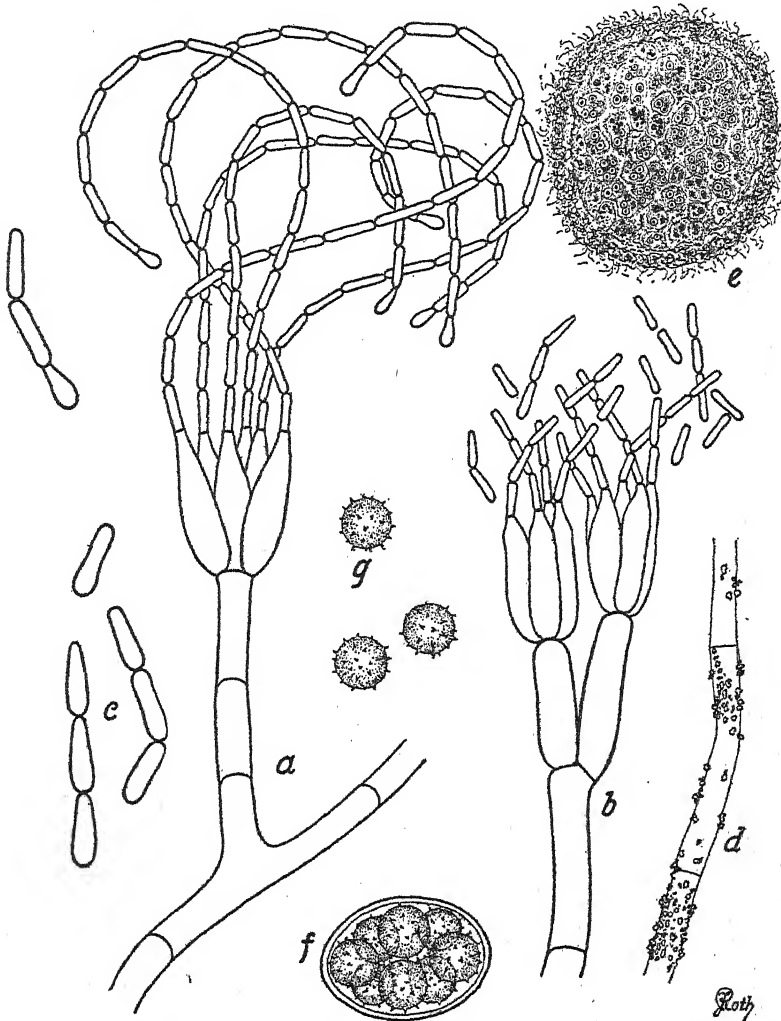
Fig. 1. *Penicillium bacillosporum*. (a) Typical conidiophore with spore chains. (b) Branched conidiophore. (c) Individual conidia. (d) Hypha with yellow granules. (e) Section of ascocarp showing asci and two-layer wall. (f) Ascus with ascospores. (g) Individual ascospores.

The asci (fig. 1, f) are spherical, oval or pear-shaped, 10–12.5×7.5–10µ. They begin to show mature ascospores within twelve days on corn meal

agar at 28° C. The ascospores (fig. 1, g) are spherical, 3.5–4µ and very finely verrucose. They are at first hyaline, but in age show an orange yellow tint. Upon germination they swell to about twice their normal size and send out one or two germ tubes.

The mycelium is hyaline, branching, septate, 2.5–4µ, and often roughened with yellowish deposits particularly about the perithecia.

CULTURE CHARACTERISTICS

The various color differences both in the medium and in the fungus mycelium on different agars is, as above noted, one of the interesting features of this species.

Corn meal agar (pH 6.8). Little aerial growth except about the very pale yellowish (18 C 1, Maerz and Paul, 1930) wefted ascocarps which dot the surface of the colony in a few days. Submerged hyphae hyaline. Reverse and medium becoming in certain areas clear bright to deep green (21 L 9 to 24 A 12). Conidia few and produced on trailing ropy hyphae chiefly near the ascocarps.

Czapek agar (pH 5.0). Growth somewhat restricted; velvety aerial felt more or less buckled. Colonies pale yellow (18 G 1) throughout with slight green tinge at extreme center; later becoming sulphur yellow (10 J 1) in the center with orange (10 K 8) droplets. Reverse at first dark and indefinite, becoming green at edges of colony (5 G 9). Both ascocarps and conidia present, but latter scant.

Potato dextrose agar (pH 4.5). Thick aerial growth, powdery to loosely velvety, persistently and uniformly pale yellow (18 F 1) with faint suggestion of green at center. Reverse dull red (6 K 11). Ascocarps and conidia comparatively abundant.

Dextrose agar (pH 4.5). Thick aerial growth, powdery to loosely velvety. At first pale yellow (18 H 1) with narrow white margin, becoming deep salmon (1 A and B 11) with deeper-colored drops (1 H 12). Reverse at first deep green (25 J 3), becoming dull red except at edges where green persists. Medium red (9 G 11). Conidia and ascocarps comparatively numerous.

Sabouraud agar (pH 4.4). Growth coarsely velvety. At first green then center area dull reddish gray (6 B 9) surrounded by band of greenish gray (29 Z 9), margin white. Reverse red (6 L 10). Ascocarps not visible macroscopically, and present only in small numbers. Conidia quite numerous.

Potato plugs. Growth irregularly velvety, dull gray green (29 Z 3) becoming yellowish (16 D 1), with margin white. Numerous conidia but few ascocarps.

The extreme range from green to red color produced in the media was

thought to be due possibly to differences in hydrogen ion concentration, the green predominating in lower, the red in higher acidities. Accordingly, transfers were made to two tubes of corn meal agar, one with the usual pH of 6.8, the other changed to 4.8. At the same time transfers were made to two tubes of potato dextrose agar, one with the usual pH of 4.5, the other changed to 7.0. After two months of growth, no differences in color production or in rate of growth have been observed.

The local and more or less spasmodic production of the bright green pigment in corn meal agar was found not to be correlated with temperature. Cultures grown at 28° C. and 40° C. showed similar coloration, and very little difference in rate of growth. The perithecia produced at the high temperature were somewhat smaller and matured ascospores at a later date than those grown at 28° C. At 52° C. no growth of the fungus occurred.

This work has been done under the supervision of Dr. B. O. Dodge, whose valuable guidance is acknowledged with appreciation. I am also indebted to Dr. Charles Thom for his courtesy in examining cultures of *P. bacillosporum* and criticising the manuscript.

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The morphological and cytological development of Meliola circinans

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(WITH PLATES 16 AND 17)

INTRODUCTION

Our knowledge of the tropical fungi rests largely upon the foundation laid by the work of Berkeley, Bresadola, Cooke, Hennings, Léveillé and Rehm. At present, with the greater facilities at our disposal, closer contact with the region and better conditions for collecting, the number of workers on exotic fungi has been greatly augmented, and our knowledge of the tropical fungous flora is rapidly increasing. While the Perisporiales have been studied from the standpoint of their morphology and classification, but little cytological work relating to members of this order is to be found in the literature. Gäumann (1922) has studied the cytology of *Lanomyces tjibodensis*. A large gap remains to be filled in this very important phylogenetic position; namely, between the Erysiphales on the one hand and the Sphaeriales on the other.

The numerous papers on *Meliola* and related genera have dealt for the most part with descriptions of new species and varieties, though in some cases the studies have been pursued with an aim toward the modification and improvement of their classification. With the advancement and application of the idea that taxonomy should be an expression of phylogeny, more detailed studies are needed to supplement those of gross anatomy. In this way only can the niceties of distinction among the groups be brought out. This type of investigation often leads to the recognition as well of more fundamental facts regarding the life and habits of the organism.

In the development of this problem I have been concerned chiefly with the series of important steps included in the formation and growth of the ascocarp. Ward's (1883) conclusions regarding the rudiments of sex organs in *Meliola* were entirely hypothetical and inconclusive. In connection with this phase I have found that true sex organs are developed, and that, with the finding of these typical antheridia and oögonia, the ideas regarding the relationship of the Perisporiales with the Erysiphales become more firmly established. The prior formation of the hyphopodium, beneath whose protection these sex organs are formed, and its development into a hood-like stroma, that incloses all but the basal portion of the later-formed ostiolate perithecium with its protruding periphyses, substantiates the ideas of Bucholtz and Von Höhnel, though contrary to the prevailing notion in regard to this outer protective layer.

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Of no less interest is the parasitic nature of the species under considera-
tion. Though haustoria have not been at any time observed, the evidence
of parasitism is convincing, and this species is found to represent the ex-
treme of ectoparasitism. It attacks the host epidermis with injurious effect
without penetrating into the cell cavities or beyond the subsidiary cells
at the stomatal opening.

The genus *Meliola* was first instituted by Fries (1825) with the species
Sphaeria? amphitricha, based by him (1823) on three of Sprengel's (1820)
species of the genus *Amphitrichum*. As first described this genus was placed
by Fries in the "Sphaeriacei," but with the statement that it is somewhat
analogous to *Erysiphe*. Later he (1830) strengthened his genus by the
addition of a second species, *Meliola Psidii*, and nineteen years later
(1849) transferred the genus to a new position, with *Erysiphe*, *Lasiobotrys*
and *Asterina*, in his group Asterinei of the "Perisporiacei."

Bornet (1851) seems to have been the first to consider the structure
of the members of this genus with other than a purely taxonomic view-
point. He adds somewhat to the knowledge of their coarser anatomy, but
contributes nothing in regard to their method of development or the
formation of their ascocarps.

To date Ward (1883) has given us by far the most extended account
of the development of *Meliola* and, in the confusion of ideas as to the
morphology and classification of the group found in the later literature,
his data are most constantly referred to, either directly or by implication.
With regard to sexuality in this genus he arrives at certain interesting
conclusions. He says in this connection, "The original pyriform branchlet
—containing in itself, so to speak, the elements of the fruit-body—after
the first division, may be considered as establishing morphologically an
'archecarpium' (De Bary, Beiträge IV, proposes to use this word as de-
noting that part of the body which becomes the ascus and pedicel in
Podosphaera) and an antheridial branch—or the latter may be considered
as containing in itself the antheridium, plus the elements of the perithecial
wall." He looks upon *Meliola* and its allies as a branch group derived from
the *Erysiphe* stem, either from ancestors of *Erysiphe*, or ancestors which
gave rise to *Eurotium* and *Erysiphe*, and considers that these forms have
developed in the tropics along lines parallel with the Erysiphaceae.

Gaillard (1891, 1892) believes that two sorts of hyphopodia can be
readily recognized, and distinguishes them as "hyphopodies mucronées"
and "hyphopodies capitées," for he says that all hyphopodia do not pro-
duce perithecia. The mucronate hyphopodia are considered as merely
hyphal branches which have their development arrested. Ward made
no distinction among the hyphopodia and believed all to be of this nature.

Growth may be resumed, as Gaillard says frequently happens, in which case one of the two opposite hyphopodia retains its habitual aspect while the other grows into a typical vegetative hyphal branch. Gaillard describes the presence òf only a single protective wall about the ascocarp and fails to find any indication of an ostiole.

Thaxter (1896), speculating upon the nature of the Laboulbeniaceae, and their possible relationship with the Hypocreaceae and other pyrenocarpous Ascomycetes, says, "It is worthy of note that the bodies most nearly resembling the characteristic antheridial cells found in this family are the 'hyphopodies mucronées' of the *Meliolae*." This assumption is doubtless largely due to the influence of Ward and Gaillard, and is based on the conception that while the capitate hyphopodia may develop into ascocarps, the mucronate develop no further, and he infers for these latter the function of antheridia.

Fischer (1897) places the *Meliolae* under the Plectascineae within the Aspergillaceae, and in association with *Testudina*, *Zukalia* and *Ceratocarpia*. Bucholtz (1897) draws critical attention to Fischer's arrangement, and disagrees with his views on the structure of the members of this genus. A well developed ostiole was observed by him to be present at the time of maturity, though in the early stages of development none was apparent. Periphyses which protruded through the ostiole at the time of maturity were also observed, but no paraphyses were found. It was seen that the numerous periphyses within the ascocarp were colorless, while the portion of those exposed through the ostiole became much thickened and brownish in color. In the young condition, he says, in agreement with Ward, that the interior of the ascocarp appears to be of a true parenchymatous nature, and that within this parenchyma tissue there appears a cell rich in cytoplasm which seems to be the ascus anlage.

Von Höhnel (1917), in studying a number of the *Meliolae* and related forms, comes to the conclusion that the thyriothecium (Von Höhnel 1910) is not a single structure but composed of two portions, a protective shield and a true perithecium. He also finds that the perithecium is not inverted but upright in its development, thus agreeing with Gaillard (1893) on this point.

Arnaud (1918) is of the opinion that the hyphopodia are not functional as sexual organs, but says that they are rudiments of perithecia and organs of absorption, and proposes to designate the capitate hyphopodia as stigmopodia. He places *Meliola* in the Dothideaceae and considers that, from the point of view of the ascocarp and ascus form, they are much simplified and probably related to the Microthyriaceae through the Wardineae.

MATERIALS AND METHODS

In the following investigation the material used, *Meliola circinans* Earle, growing upon *Carex* sp., was gathered by Professor R. A. Harper, in the vicinity of Miami, Florida and through his kindness furnished to me for study. The fungus, upon portions of the host, was fixed in the field, when gathered, in Flemming's medium fixative. As soon as practical this was embedded in paraffin so that up to this stage there was no delay in the sequence of preparation. In the further preparation of the material for observation sections were cut, and mounted in the usual manner, from 5 to 7.5µ in thickness, varying with the condition of the material, and feasibility of obtaining thin sections. Due to the hard outer covering of the fungous fruit and the heavy cutinization of the epidermal cells of the host, thinner sections did not prove practical. In staining the Flemming triple method was used as giving the greatest amount of contrast and clearness for observation.

Certain ambiguities have crept into the terminology employed in the discussion of the ascomycetous fungi. The term *ascocarp* is used throughout this paper to designate the entire ascus bearing fruit. In so doing, it is with the idea that the term is a general one applicable to any ascus producing fructification, of whatever type, whether apocarpous, pyrenocarpous or cleistocarpous, and also whether simple or compound.

The term *perithecium*, too frequently loosely used to designate the entire fructification, is here applied in a more restricted sense. Properly the perithecium is a product of the gametophytic stalk cells from which the sexual reproductive organs also develop, and is an inclosing protective envelope whose initiation is evidently closely correlated with the formation of these organs. The perithecium includes normally several layers, as pointed out by De Bary (1884) and Harper (1896, 1905) in their studies on the structure and development of the mildews, an outer cortex, when its functions are not usurped by a substituting tissue as seems to be the case with the Dothideales, and an inner nutritive layer in association with which may develop the paraphyses and periphyses.

Until the real relation of sporophyte and gametophyte in the ascocarp of the *Meliolae* and other Ascomycetes is clearly recognized certain general terms will prove useful. For the portion within, the term *core* as used by Ward (1883) seems better than "nucleus" or "kernel" sometimes found in the literature for denoting in a general way the portion contained within and bounded by the perithecium. In the same way it is frequently convenient to designate as *cortex* the portion of the ascocarp outside this core. When more specific distinctions are required the appropriate names for the various portions must be used.

MYCELIAL DEVELOPMENT

Meliola is a genus of very wide distribution throughout tropical and subtropical regions of both the eastern and western hemispheres. Within this range a great number of species are found growing upon a wide variety of host plants, but almost entirely restricted in habitat to their leaves, and usually appearing upon these when they are in a mature or nearly mature state.

The vegetative development begins, according to Ward (1883), with the germination of any one or several cells of the pluricellular spore on the surface of the host. Following germination the hyphae spread in a diverging radiate manner over the leaf surface and form a dark incrusting layer, the maculae of Fries (1823) and Montagne (1842). Frequently, in the younger and smaller maculae, the remains of the initiating spore can be found in a central location. The evidence seems to show that each of these areas is the result of infection by a single spore, except in cases when numerous infections take place and adjacent growths become confluent. However, if it is possible for any one or even all of the cells of the spore to take part, the hyphae which compose a single macula may be the product of more than one of these cells. In view of the peculiar nuclear distribution within the developing spore, such as I have described in the following pages, and the condition found by Dodge (1927, 1929) to exist in the genus *Neurospora*, it would seem that further work and observation upon spore germination and nuclear activity in *Meliola* is very desirable.

Considering the presence of ascocarps as a sign of maturity, it is found that the maculae of *Meliola circinans* Earle vary from three to five millimeters, rarely more, in diameter. They have a slight tendency toward an oval shape due to a slight inhibiting effect of the raised longitudinal leaf veins upon the hyphal growth. In different species these maculae vary in size, regularity and form, and constitute the so-called subiculum in association with which the ascocarps develop.

Though ascocarps usually begin to appear on the maculae when they have reached a diameter of approximately three millimeters, they will occasionally be found on somewhat smaller spots. Their formation proceeds from the center outward. At the beginning of this period, in consequence, there is a margin of hyphae upon which they are not yet evident. With increase in size, and the accompanying maturity of a larger area, ascocarp production progresses outwardly in all directions. When a diameter of about five millimeters has been attained hyphal growth seems to cease, but ascocarp formation continues until they are at last found near the outer limit of the spot. One would judge from appearances that asco-

carp production continues at the center, as well as over the other portions of the maculae, for some time. Finally the center may be readily broken away while the marginal portion remains still quite firmly applied to the host. The character of the hyphae, method of branching, etc., are well known and need no detailed description.

Besides the usual type of branching, sterile, rigid, simple or branched hyphae, the familiar upright setae, may be produced from various portions of the vegetative growth. In some species these are found more numerous about the base of the ascocarp and in many cases irregularly disposed upon its surface. In our species they appear scattered upon the vegetative hyphae, as simple, straight, upright branches that taper to an acute point and measure from 400 to 800μ in length and about 12μ wide at the base. Only rarely have they been found to make their appearance upon the surface of the ascocarp (fig. 9), nor are they at all numerous about its base. This latter condition is undoubtedly correlated with the absence of a well formed hyphal cushion or "hypothecial disk" such as is usually more or less pronounced beneath the ascocarp in species where basal setae are numerous. Bornet (1851) figures these setae in such numbers and regularity about the base of the ascocarp as to emphasize the Friesian idea of their similarity to the appendages of the Erysiphaceae, particularly in the case of *Meliola furcata* Lév., where the ends are ornately branched much as in *Microsphaera*.

More or less regularly arranged short side branches also develop in large numbers. Each consists at first of a small stalk cell and a slightly enlarged end cell. These are the familiar hyphopodia, or morphologically arrested branches, and partake of the nature of appressoria. It seems that, partially at least, nourishment is obtained through their agency. Their under surface is thin-walled and in close contact with the surface of the host. Further than this these hyphopodia are directly associated with ascocarp formation and the reproduction of the fungus.

The hyphopodia are potentially capable of further growth though the great majority do not develop beyond the condition just described. Setae may develop by their upward prolongation. Renewed growth in the original direction may take place and result in ordinary vegetative hyphal branches. If, however, the terminal cell enlarges somewhat and the first septation is diagonal and is followed with an increase in the number of cells by meristogenous development we have formed the capitate hyphopodium of Gaillard and the anlage (figs. 1, 2) of an ascocarp. I find no occasion for a morphological distinction between types of hyphopodia other than one of ultimate development.

Hyphopodia notably similar in position, development and function

have also been described by Doidge (1920) for the related genus *Amazonia*, under the name *Meliolaster*, as well as by Stevens (1927) for *Irene*, *Irenopsis* and *Irenina*.

<div align="center">HOST RELATIONS</div>

The encrusting type of growth developed by the *Meliolae* upon the leaf surface of a vast number of tropical and subtropical plants raises the question as to their saprophytic or parasitic habit and relations to the host substratum. It has never been adequately shown whether they are primarily saprophytic and dependent for their food supply upon materials accumulated from the air or excretions of leaf infesting insects, or, if parasitic, the extent of their parasitism and the amount of injury they may cause.

It has been generally assumed that the growth upon the leaf surface including the so-called subiculum associated with ascocarp production, constitutes the vegetative stage. This incrustation is, in many cases, easily separable from the leaf surface upon which it may be thriving, while in others separation seems to be accomplished with more difficulty. The xerophytic nature of the fungous crust, composed of heavy-walled hyphae, except that at the time of growth they remain lighter at the tips for a brief period, would seem to preclude the assumption of any active attack on the leaf surface. The literature contains but meagre reference to the ability of superficial fungi, or any others, to attack heavily cutinized cell walls. The entrance of haustoria or penetrating hyphae through this protective layer has been, however, much studied.

Bornet (1851) questions the real parasitic nature of *Meliola*, and is of the opinion that the lesions, observed occasionally on the leaves upon which it is found growing, are due to the action of numerous mites whose remains one often finds. With this Gaillard (1892) agrees, and adds that by examining numerous leaf sections he has satisfied himself that the *Meliolae* are entirely superficial, and do not in any way injure the tissues of the plant upon which they grow. Berkeley (1857), without direct evidence, is very positive as to the injurious effect of the fungus on the host.

Ward (1883) says that on the under side of the hyphal wall, where in contact with the host, thinner spots, lacking coloring matter, will be seen where the protoplasm is more nearly in connection with the outside. These bright spots are the points of attachment to the epidermis, and may be regarded as haustoria of a very rudimentary nature.

In all, Maire (1908), Arnaud (1914, 1918) and Doidge (1921) have demonstrated the presence of haustoria in sixteen species of *Meliola*. In

two of these the haustoria penetrate to subepidermal cells in the same manner as do those of *Asterina*, though remaining simple and unbranched. The fungus was found to be easily separable from the host in the case of *M. bifida* Cke., and Doidge was unable to show the presence of haustoria in connection with this species. Ward found no evidence of haustoria in the unnamed species of *Meliola* which he investigated, though he (1882) had no difficulty in clearly demonstrating their presence in *Asterina spisa* Syd., at an earlier date. Gaillard says that after examining numerous leaf sections he has satisfied himself that the *Meliolae* are entirely superficial, but he does not name the species he sectioned.

In *Meliola circinans* Earle I have found no evidence of the presence of haustoria, and the fungus is to all appearances entirely superficial. The hyphae are in intimate contact (figs. 1, 4, 7, 8) with the epidermis and follow closely all its irregularities. Also the cell walls of the hyphae are seen to be markedly thinner wherever this contact is maintained. Stomatopodia (fig. 4) may enter and fill the deep cavities within which the stomata are located. This plug or foot, however, does not pass between the guard cells, but terminates at this point where it is in contact with them. It develops no further, and no fungal growth appears in the substomatal cavity. As pointed out by Theissen (1916) for *Stomatogene* (*Dimerium*) *Agaves* (Ell. & Ev.) Theiss., where a similar situation occurs, we have the natural question as to whether the fungus should be considered as superficial (oberflächlich) or as really penetrating (eingewachsen) the host. In view of the form of the plug in this species of *Meliola*, which is indented at its base immediately over the stomatal opening but closely appressed to the outer walls of the host cells, it appears that a purely superficial relation must exist between fungus and host.

Where the fungous hyphae and host are in contact it is seen that, coincident with the hydrolysis of the heavily cutinized wall, the first change to appear is a slight swelling accompanied by an irregular reduction in staining capacity (fig. 4) of the host wall, thus showing evidence of a chemical as well as physical alteration. This is followed by evidence of digestion which results in the irregular thinning (fig. 8) of the host wall. While the swelling which takes place is very slight, the succeeding reduction in thickness is well marked, with the hyphal filaments of the parasite closely fitted into all resulting depressions and irregularities.

We have then, from the evidence at hand, three grades of parasitism represented in the genus *Meliola*. Most frequently haustoria of a simple type are formed. They penetrate the cuticle of the host and form an haustorial vesicle in the cavity of the epidermal cell. There are occasional species which develop haustoria of the *Uncinula salicis* type (Smith,

1900) which, though still simple unbranched structures, penetrate to the cell cavities of the mesophyll region. And lastly there are species, wholly superficial in character, which fail to come into direct contact with the host cytoplasm, but in some way corrode the epidermal cell walls more or less and, from the evidence of degeneration products (fig. 8) which appear within the epidermal cells, cause some real though not deep seated injury to the host. This corrosion process may be effected by any portion of the fungous hyphae in contact with the cuticle.

ASCOCARP INITIATION AND DEVELOPMENT

As pointed out above, the ascocarp is the entire ascus fruit whereas I shall use the term perithecium to signify structures having the same origin as the envelope in the cleistocarpous Erysiphales. In the genus *Meliola* the ascocarp initials are first seen as short two-celled lateral branches growing from the sides of the vegetative hyphae to which Gaillard (1891) has given the name of hyphopodia. As previously noted Gaillard considers these hyphopodia to be of two sorts which he distinguishes as "hyphopodies mucronées" and "hyphopodies capitées." In this he has been followed by Thaxter (1896) and Gäumann (1926), as well as a number of systematists who use the characteristics of these two stages of development in species diagnosis. That these hyphopodia are equivalent to one another, as far as early development is concerned, there seems to be no doubt, though it is true that many of these structures seem destined never to develop further than the two-celled condition, and that but a proportionately small number are capable at any one time of developing into ascocarps.

The hyphopodia of the species under consideration are typically two-celled at the time of their early development. The enlarged rounded terminal cell is attached to the hyphal branch from which it originated by a single short stalk cell. This characteristic seems fairly constant for the genus, though this stalk cell has been reported as sometimes lacking. The terminal cell of the hyphopodium is in close contact with the surface of the host and, as previously suggested, may have the nature of a rudimentary appressorium. Those which continue development seem to have in many cases an association with the stomata of the leaf, and after reaching some greater size produce a foot or plug (fig. 4) which fills the epidermal depression between the subsidiary cells but not the guard cells. This plug does not penetrate the stomatal opening nor does it produce hyphal branches for this purpose. Apparently it serves only to secure a better contact with the surface of the host.

When it develops further] as the anlage of an ascocarp, the initial

growth of the hyphopodium takes place in a centrifugal manner parallel
to the plane of the leaf, and results in the formation of a lenticular group
of cells. The first division of the terminal cell of the hyphopodium, as
described by Ward (1883), takes place by the formation of a septum
vertical to the plane of the mycelium and leaf and passes diagonally across
the cell with a slight curve. Due apparently to the nature of this first
septation, growth for a time results in a disk or plate with a subradial-
subhelicoid appearance which, however, is soon lost as development pro-
ceeds. The exposed cell walls are thickened and dark colored in a manner
similar to the walls of the regular hyphae. The vertical walls are heavy
and colored for only a short distance below the exposed surface (figs. 3, 4, 5)
and become rapidly as thin and colorless as the lower walls. This peltate
stromatic growth is a purely vegetative structure, the formation of which
undoubtedly takes place in the manner described by De Bary (1884) as
meristogenous, rather than symphogenous.

In *Meliola* ascocarp initiation is not synonymous with perithecial
initiation, and the latter does not begin till the growth of this stroma, as I
shall class it, has proceeded far enough to produce a protective cover be-
neath which further developments take place.

Ward expressed the view that the initiation of the fruit structure of
Meliola came about through a fusion, or at least a contact, of the first two
cells formed by the hyphopodium. One of these he considered as having the
nature of the "archecarpium" of De Bary, being the anlage for the inner
structures including the ascogonium and asci. The other he believed to be
the anlage for both antheridium and perithecial wall. Thaxter (1896), as
previously noted, speaks of the "hyphopodia mucronées" as resembling
the antheridial cells found in the Laboulbeniaceae. This statement seems
to carry the implication that he considers Gaillard's (1891) mucronate
and capitate hyphopodia to be the two sex organs, or at least to have in
some degree their function. Ryan (1926) follows the ideas presented by
Ward.

I find that under the protection of the young stroma, which is peltate
in this early stage, two short stalks arise from the side adjacent to the
original stalk cell of the hyphopodium. One of these is antheridial in its
nature while the other is oögonial. These (fig. 3) are the true sex organs.
They are definitely of the nature described by De Bary (1863) and Harper
(1895, 1896, 1905) for *Sphaerotheca*, *Erysiphe* and *Phyllactinia*, the only
difference being one of orientation, and in the size of the antherid which
is longer. They are usually found growing in a position parallel instead of
perpendicular to the leaf surface. This is due to their point of origin and
relation to the shielding hood of the stroma. Rarely they tend to assume

an upright position when the curvature of the protective stroma is such as to allow them sufficient space.

Oögonial and antheridial development seems to take place simultaneously, and the branches from which these organs are derived have a point of origin very close to one another. The stalk cells from which the sex organs arise are much shortened, their breadth being greater than their length. From its short stalk the oögone develops as a much enlarged, oblong-oval cell with a single large nucleus and a dense protoplasmic content. The antherid is slightly longer, more slender, nearly cylindrical, uninucleate, and has a slight tendency toward a spiral form. The sex organs of *Meliola* are Erysiphaceous in character, but protected, as described, by the small peltate hood. Thus the oögone and antherid are closely associated in origin as in the Erysiphaceae, and, as the young stromatic growth is attached to the vegetative hypha by a single stalk cell, the *Meliolae* must be necessarily homothallic.

The perithecium begins its development by the growth of hyphae from the stalk cell immediately below the oögone. These hyphae also grow in a horizontal direction, at least in their early stages, following the general oögonial contour. Certain of them may originate from the stalk cell of the antherid, but these if present are clearly not so numerous as the others. Due probably to the fact that a protective cover is already present, these hyphal filaments do not form the intimate contact with the oögone during their early development that has been described for members of the Erysiphaceae.

To accommodate the growth of antherid, oögone and perithecium the overgrowth of stroma increases and assumes at this period a hemispherical form. Up to this time the stroma is usually but one cell in thickness, but at this period or shortly after, as shown (fig. 4) in median vertical sections, this growth increases to a thickness of two cells by the formation of an inner layer. At the side opposite the hyphal connection, where it is in close contact with the host, the stroma becomes three or four cells thick. This extra thickening projects inwardly toward the basal center of the ascocarp. As growth proceeds this basal stromatic thickening is extended around the entire ascocarp, and with the ascogenous tissue as a center tends to change the orientation of the latter. At no time, however, does this stromatic ingrowth entirely close together beneath the ascocarp, and the stroma retains its flammeaceous form from now up to the time of ascocarp maturity. At the basal center the thin-walled perithecial cells are at all times in contact with the host.

With the increase in size of the ascocarp greater space is provided for the developing perithecium and ascogonium through the intercalary

growth of the stromatic hood. This is accomplished, however, without any material change in the thickness of the stroma. The ascogonium elongates (fig. 4) as a horizontal filament, and becomes divided into a short structure of uninucleate cells. The terminal of these retains for some time the shape of the oögone but, as growth proceeds, is gradually reduced in size. After attaining a length of three or four cells, the ascogenous hyphae begin to make their appearanace as side branches. The first to develop grows from the penultimate cell of the ascogonium while the second seems to be usually the product of the third cell. Both grow from the distal ends of the parent cells so that the ascogonium, with the young ascogenous branches, has the appearance of a young hyphal shoot with a large terminal cell. Whether this large cell is capable of further growth, or whether more than two of the ascogonial cells produce branches, I am uncertain.

The cells of the core at this time are relatively large, and, being compressed in their rapid growth and confined position, assume somewhat of a pseudoparenchymatous appearance, particularly (fig. 5) when observed in cross section. During the young stages the ascogonium and ascogenous hyphae occupy a central spherical region. Their cells are all uninucleate, except as nuclear division involves a temporary increase. I have not found stages showing nuclear fusion in the oögone, nor nuclear migration from the antherid. The nearest approach to this latter phase that I have seen is an oögone (fig. 3) containing apparently a fusion nucleus and an associated antherid within which the most careful focusing of the microscope failed to reveal any sign of a nucleus.

At the same time the ascogonium is developing the perithecial structure is also continuing its growth about the inner surface of the, now flammeaceous, stroma. The cells of the outer perithecial wall, which is the first to be formed, appear in longitudinal section more slender and elongate (fig. 6) than those of the other structures, and its completion is rapid. A comparison of tangential and radial sections shows that the cells of this perithecial wall become flattened in much the same manner as those of *Phyllactinia* described by Harper, and have a similar appearance to them except that their walls remain unthickened. The development of the inner perithecial layer follows closely upon that of the outer. This also has its origin in the base of the perithecium, and its growth is directed upward about the sides of the increasing cavity. The cells of this layer, unlike those of the outer, are large and more nearly isodiametric. They are rich in cytoplasmic content, and variable in the number of their nuclei.

From a position slightly over half way up the inner portion of the perithecium (fig. 9), and upward toward the apex, branches, the periphyses, are produced from the inner layer and grow across the upper por-

tion of the cavity. Their ends meet and overlap somewhat, with the result that this region is more or less occupied for a time. As this growth has been taking place, the ascogenous hyphae have continued their development over the inner base of the perithecium. Branches from these grow upward and begin the development of the first asci. Among these first asci to be formed there are seen also a few scattered paraphyses which have their origin in the perithecial base. The ascogenous hyphae are uninucleate, and the asci develop from the penultimate cell (figs. 10, 11) through the typical crozier stage. The first few to appear remind us of Ward's description for they are seen as cells which "maintain their large size and upright arrangement" in the central part of the core. They are undoubtedly the same as the cells seen by Ward (1883) and considered by him as constituting the ascogonium.

There are seldom more than two or three mature asci to be seen in any one section of an ascocarp, but numerous and varied early stages are also present showing that their production must continue for some time. The growth of the comparatively large asci with their large spores has a marked effect upon the entire inner structure of the ascocarp. With the increased spread of the ascogenous hyphae and the attendant ascus development, the inner perithecial layer becomes much flattened until its cells appear in section as a thin layer of shrunken, elongated cells poor in cytoplasm. The entire perithecial structure seems to serve as nurse tissues, and to become more and more compressed as development proceeds. The draft of material for nourishing the ascogenous hyphae and the developing asci may even extend in some degree to the inner stromatic layer. Thus all parts of the ascocarp cortex, except possibly the outermost protective layer of heavy walled cells, may contribute to their maintainance and growth, and serve in a sense as nurse cells.

Paraphyses make their appearance during early ascus formation, and are present (fig. 9) from that time through the active life of the ascocarp. At no time, however, are they numerous but remain few and scattered among the asci. They are never straight and regular in their arrangement, but grow upward as slender unbranched, twisted and bent filaments of several cells with thin walls throughout their length. In those that appear oldest the cytoplasm is very irregular in its staining quality and the size and distribution of its vacuoles. The nuclei of these are elongated and appear to be in a state of degeneration. In contrast, the younger newly formed paraphyses have a homogeneous cytoplasm and normal, spherical or slightly ovate nuclei.

As the ascocarps increase in size and the central cavity enlarges, the filaments growing into the upper region from the inner wall of the peri-

thecium become more slender. Where they formerly overlapped they now show signs of separation. This takes place first in their basal region and progresses upward. As this separation continues (fig. 9) these filaments, the periphyses, all tend to become directed upward toward the apex of the ascocarp. Those reaching farthest upward push apart the cells of the perithecium and stromatic hood at this point. The tips of the periphyses then protrude, and their terminal cells substitute (fig. 17) for the displaced portion of the stroma. The exposed ends become rounded, slightly enlarged and develop thicker, dark-colored walls which match well, except in size, the outer walls of the stromatic cells. This condition undoubtedly accounts for previous failures to observe the protruding periphyses. Ward observed, in an unnamed species of *Meliola*, a slight papilla at the apex of the ascocarp. He also noted that the cells of the inner wall converge toward this spot, and concluded that this is at least a weak point through which spores escape. Bucholtz (1897) found that in *Meliola corallina* Mont., *M. amphitricha* Fr., and *M. cymbisterma* Mont., there is a well developed perithecial ostiole from which periphyses were seen to protrude at the time of maturity. Aside from these statements of Ward and Bucholtz we find no direct reference to ostiolar development in the extensive literature on this genus.

With the approach of complete maturity, the perithecial cells at the base of the ascocarp, where unprotected by stroma, and in contact with the host, develop thickened walls. These are nearly as heavy and dark colored as those of the exposed stromatic layer. At the same time the ascogenous hyphae have increased so that they are distributed over the enlarged base of the cavity. With this growth they have become more slender, and the various stages in ascus formation appearing in each section are more numerous. Paraphyses are still to be found sparsely scattered among the asci. In the upper portion of the cavity the periphyses are seen to have lost much of their original protoplasmic content and to become more consolidated into a crown or cap of hyphae converging toward the apex of the ascocarp. The formation of this perithecial ostiole as a definite place of dehiscence is in agreement with the findings of Bucholtz. That the ostiole does not attain complete development until the first formed asci are approaching maturity and nearly ready for the discharge of their spores is also in harmony with his observations.

ASCUS AND ASCOSPORE DEVELOPMENT

During early ascus development the hyphae from which they originate are short and composed of cells with a relatively large diameter and a single, prominent, though not large, nucleus. The first few asci to appear

form a group of large, upright cells occupying the center of the ascocarp. These have developed from the first-formed, short ascogenous hyphae seated upon the portion of the inner perithecial wall at the base of the ascocarp. From the cells of this wall, which are quite large at this period, a few scattered paraphyses are found growing upward among the asci, and of about the same length. The asci pass through the typical crozier stage (fig. 10), in their early development. The ascogone becomes unrecognizable among the growing hyphae during this early period.

During the later growth of the ascocarp the removal of reserve materials results in the somewhat diminished thickness of the perithecial wall and this, together with the increased size of the fruit body, serves to increase the size of the inner cavity. At the same time the developing asci are brought, as a consequence, into a relatively lower position. The ascogenous hyphae, in continuing to spread over the enlarged ascocarp base, become more attenuated and their branches more numerous, intertwining and difficult to follow. With the smaller diameter of their cells, their nuclei are also slightly diminished in size. Under this condition, however, as the crozier is being formed, the three or four cells nearest the end of the hypha so engaged increase in diameter, and the nucleo-cytoplasmic ratio is maintained by a concurrent increase in the size of the nuclei. It is thus seen that the continued production of relatively large asci is not dependent entirely upon growth after ascus formation, but is related in some degree to a stimulus present within the hyphal filaments at the time of ascus initiation.

The crozier is formed in the usual manner, and after the enlarged, broadly ovoid ascus cell becomes (fig. 11) two to three times longer than broad, and about one forth the length of a mature ascus, its two nuclei fuse. The fusion nucleus is very large, and shows evidence of a considerable growth before the first division takes place. It occupies a position near the center of the ascus and attains a size approaching two thirds the diameter of that cell. The cytoplasm is homogeneous throughout the entire ascus.

As the ascus elongates and becomes clavate in form the first nuclear division takes place, and this is soon followed by the second and third divisions. As is the case with many ascomycetes, the first division takes place in the general direction of the long axis of the ascus, or in a slightly oblique manner. The two daughter nuclei remain near the center where the second division also takes place. In this the direction of division is oblique, and the four nuclei, still retaining a central location, prepare for the third division. The resulting eight nuclei, in remaining likewise in the central portion of the ascus, make it difficult to trace their relationships to one another.

Though, ordinarily, but two spores (fig. 14) are found in the mature ascus, the usual eight nuclei are to be seen prior to spore formation and all take part in early spore development. Following the last nuclear division there is an arrangement of the nuclei in pairs, in such a manner that if median transverse sections of an ascus are seen but four would be in the field at one time. While in this position the four spores are cut out.

In Ward's description of spore formation no mention is made of nuclear conditions. According to him the procedure is a progressive one in which the first act is a longitudinal cleavage dividing the ascus content in half. This, he says, is followed by a second cleavage, likewise longitudinal, but at right angles to the first. With this my observations do not agree for I find that the spores are cut out simultaneously as four fusiform cytoplasmic bodies. These each contain two of the eight nuclei (fig. 12) located in a median position. In the act of spore delimitation the greater portion of the cytoplasm is included within the spores, and only a very small amount of residual epiplasm remains in the ascus. Throughout ascus development the entire cytoplasmic content remains very homogeneous, and there are no largely vacuolated regions such as are common in those species that produce proportionately smaller spores and a larger amount of epiplasm.

In the delimitation of the four spores within the ascus, instead of the usual eight, together with the cutting out of the cytoplasm so as to include two of the eight nuclei within each spore, we are reminded of Wolf's (1912) first report of such an occurrence where he describes a similar condition for *Podospora anserina* (Rabh.) Winter. The next to bring to our attention a like feature is Dodge (1927) who found that in *Neurospora tetrasperma* Shear and Dodge, the cutting out of four binucleate spores within the ascus is the normal event. To these may be added the variation which Dodge (1928) later reports when he says that in *Keithia Chamaecyparissi* Adams, the two spores of its asci are each cut out with four nuclei. In other cases, so far investigated, where fewer than eight spores are regularly formed, such as that of *Phyllactinia corylea* (Pers.) Karst., investigated by Harper (1905), *Verpa bohemica* (Krombh.) Schröt., by Komarnitsky (1914) and *Laboulbenia chaetophora* Thaxt., and *L. Gyrinidarum* Thaxt., by Faull (1912), it has been found that some of the nuclei degenerate prior to spore delimitation and only those retaining their normal size take part in spore development. In these latter the usual uninucleate spore is formed and the degenerating nuclei gradually lose their identity within the epiplasm.

When the spores are first formed in *Meliola circinans* Earle, there are four in each ascus (figs. 12, 13, 14) but as they proceed in their develop-

ment two of these grow in size at the expense of the other two. As first cut out the four spores are of equal size. The growth of two of these is rapid, while at the same time the other two diminish laterally and become thinner as the others become larger. Finally only two remain, the last trace of the others having disappeared. Though I have seen instances where all four spores of an ascus have completely matured, such occasions are very rare. I have never found cases where numbers other than two or four develop.

The individual spore (figs. 14, 15, 16) in our species is five-celled at maturity, and at this stage always contains six nuclei, two in the middle cell and one each in the others. This nuclear number is arrived at through normal division and without the loss of any nuclei by degeneration. The formation of the several spore cells and their nuclei is achieved by a progressive development. After the simultaneous division of the two nuclei in the young single celled spore the four daughters become arranged in a median line, one from each pair approaching the end of the spore nearest to it. The remaining daughter nuclei retain a position near the center of the spore in about the same location as their parents. Just prior to the next nuclear division the end cells of the spore are formed by the development of cross partitions. In this way a single nucleated cell appears at each end of the spore, and a very large binucleated cell is left in the center. The nuclei of the terminal cells do not divide again during spore growth. The two nuclei of the large central cell, which is destined to develop into the three that remain to be formed in the spore, then both divide (fig. 15) in a diagonal direction. With this division the formation of the six nuclei of the mature spore has been achieved. Two walls are then formed cutting off the second cell from each end with single nuclei and leaving two nuclei, granddaughters of each of the original, in the central remaining cell.

I have also seen sufficient evidence to lead me to conclude that a reversal of the above mode of spore septation may take place, and that in this event daughter nuclei of original nuclear pair will be present in the central cell instead of their granddaughters. This seems more likely to occur when the spore breadth develops at a proportionately greater rate than its length. In this event the original pair of nuclei divide diagonally, and with the cutting off of the central cell, which in this case is the first one formed, a daughter of each is included. As the spore continues to elongate the other two nuclei then divide, move into alignment and are then separated from one another by cross partitions. In this way the two cells toward one end will have single nuclei that are granddaughters of one of the originals while the two toward the other will have single nuclei that are granddaughters of the other of the original pair, and the center cell will contain two nuclei, a daughter of each member of the original pair.

As the two spores of the ascus increase in size their adjacent sides are somewhat flattened by pressure, and the nuclei (fig. 14) of each become arranged in a line on the side of the spore away from its neighbor. With continued growth each cell of the spore becomes somewhat rounded, resulting in a slightly constricted appearance at the location of the transverse walls. The terminal cells become obtusely rounded or slightly apiculate. As the condition of maturity approaches the cell walls (fig. 16) become much thicker and dark colored. This dark brown color of the mature spore becomes so dense as to obscure almost completely the cytoplasmic content.

The ascus wall is thin at all times, and, as the spores develop, becomes distended and fits closely about their contour. It readily tears away at the base when mature, and often continues to invest (fig. 14) the paired spores for sometime. These may be seen in the ascocarp cavity ready for discharge and covered by the remnant of the ascus wall that is so thin as to be barely visible. On breaking or tearing in any other region the spores escape and separate in the cavity leaving the fragile collapsed ascus behind.

Ordinarily the spores are discharged through the perithecial (fig. 17) ostiole. As the older fruits may break away from the substratum and the base of the ascocarp is unprotected by the stromatic growth, instances are not rare where the exposed perithecium by breaking allows the spores to escape through the more lightly protected base. This condition is, in all probability, the explanation of Bornet's conclusion that normal dehiscence takes place by the formation of a circular rupture about the base of the ascocarp, and that the top and sides of the "concepticle" serve as a lid.

DISCUSSION

The historic basis in the classification of the Ascomycetes has naturally been to a large extent one of gross morphology. With the increased study of the more minute details of structure, cell fusion and nuclear behavior connected with their life history, the finer distinctions in the evidence for phylogenetic relationships have gradually emerged. In the genus *Meliola* we find for the first time among the Perisporiales the true oögone, as originally described by De Bary for the Erysiphales. This organ as I have shown in the present paper, appears as an enlarged uninucleate cell, beneath the protective stromatic shield, in close association with a more or less spirally twisted antherid. It is usually, though not always, seen growing in a position parallel with the surface of the host. This orientation is due, in part at least, to the confinement of these organs beneath an incrusting stroma. Hyphal branches grow from the stalk cell bearing

the oögone, develop much as in the Erysiphaceae, and surround that organ. A perithecium is produced in the same manner as has been reported for *Erysiphe, Phyllactinia* and *Sphaerotheca*, except that it matures into a true ostiolate structure rather than a cleistothecium, and is located under a thin flammeaceous stromatic layer whose cells are pushed aside to allow the ostiole to become exposed and the periphyses to protrude.

Harper (1905) mentions the occasional presence in the young asco-gonium of *Phyllactinia corylea* (Pers.) Karst., after fertilization, of a small nucleus whose fate he was unable to determine. This was but one-third the diameter of an ordinary nucleus, or even less. The suggestion is made that possibly the first division in the oögone may give rise to a super-numerary nucleus similar to that found in the germination of the zygospore of certain algae. A similar nucleus has since been observed and figured by Winge (1911) in the oögone of *Sphaerotheca Humuli* (DC) Burr., but prior to migration of the male nucleus. As shown in his figures, one of the two thus formed enlarged to become the oögonial or egg nucleus while the other becomes reduced in size. Whether these small nuclei of Harper and Winge are identical must be considered at present uncertain. Their po-sition and degeneration would seem to indicate that such is the case. The fact, however, that in one case this nucleus was found subsequent to fertil-ization while in the other it is reported as found in the unfertilized egg may cause some feeling of doubt.

I have found a similar small nucleus located below the large fusion nucleus in the female sex organ of *Meliola*, and, from its appearance, un-doubtedly in the process of degeneration. In view of the phylogenetic development of the Ascomycetes, and the reduction of the archicarp to the single celled oögone, it seems not improbable that this superfluous nucleus can best and most simply be accounted for as vestigial. It seems not at all unlikely that in the development of the short oögonial filament, when the terminal cell increases in size, nuclear division may sometimes take place. As no cross wall is formed, the oögone begins its development with two sister nuclei one of which becomes functionless and degenerates while the other serves as the active nucleus of the egg. In those forms in which the archicarp possesses a trichogyne and conductive cells beyond the egg cell such development is carried even further and is accompanied by septation. With the reduction of this organ it is not unnatural that at times super-numerary nuclei may be found. Dr. Illo Hein tells me that in his studies (1927) of *Sphaerotheca Castagnei* Lév., he found a similar degenerating nucleus sometimes present in the female sex organ. The length of the tri-chogyne and extent to which the conductive cells are developed appear to be a matter of ordinary growth and to depend on the ecology of the fungus.

In a similar way we can also account for the controverted nucleus found by several workers in the trichogyne of certain Florideae. In those cases where a trichogyne is present, whether in the Florideae or Ascomycete, its nucleus or nuclei degenerate after passage of the male nucleus and not before.

With the removal of a considerable number of genera from the ranks of the Perisporiales this seems to be gradually becoming a depauperate order. Apparently these revisions are due, in part at least, to the recognition of the presence of an ostiole in an accumulating number of species. For example, this together with other factors led Arnaud (1910) to remove to the Sphaeriales such genera as *Limacinia*, *Capnodium*, *Perisporium*, *Zuklia*, *Meliola*, *Asteridium* and several others from their old position.

Theissen (1913, 1917) has instituted a new order, the Hemisphaeriales, to receive genera largely Perisporiaceous in their nature. These views have been accepted in part by Gäumann in his "Vergleichende Morphologie," as well as by C. W. Dodge in his revised translation of that work. They have both allowed *Meliola*, however, to remain in its old position among the Perisporiales. Later Arnaud (1918, 1925) revised his earlier conclusions and has suggested the removal of *Meliola*, together with *Amazonia* to the Dothideales. While it may seem expedient to divide these numerically rapidly increasing groups, the recent subdivisions seem to be the cause of unnecessary confusion. Either the members of the Perisporiales should be entirely distributed among other orders or the definition and boundaries of this order should receive a much needed emendation. The question is one of phylogenetic conception.

Much of the confusion of the past is found to hinge upon a misconception of what constitutes a perithecium, and the loose use of that word in reference to the outer portion of an ascocarp when a stroma is present. The genus *Meliola* offers a good illustration as few species descriptions appear in which the outer fruit surface is not designated as the perithecium, though in reality it is the surface of a flammeaceous stroma beneath which the perithecium is hidden. Setae appearing upon the surface of this ascocarp are spoken of as "perithecial setae." As they are outgrowths from the stromatic surface they must have the same general origin as the hyphal setae, and to speak of them as perithecial setae gives a wrong impression. The setae of *Meliola* may be produced from strictly vegetative hyphae, from its hyphopodia or from the stromatic surface of the ascocarp, and in some species they are developed from all three localities. All are vegetative in their origin. In spite of the similarity in appearance, the ornately branched setae of *Meliola furcata* Lév., which appear

about the ascocarp, have their origin in the stroma while those of *Microsphaera* are outgrowths from a true perithecial wall. The latter have their ultimate origin in the stalk cell of the oögonium which produced this perithecium.

Between *Meliola* and the genus *Asterina*, which Theissen places in the Hemisphaeriales, we find *Amazonia* with, as pointed out by Doidge (1920), intermediate characteristics. This latter genus is associated with *Meliola* in the Meliolineae by Stevens (1927), classed among the Hemisphaeriales with *Asterina* by Theissen and Sydow (1917), and among the Dothideales, together with *Meliola*, by Arnaud (1918). Theissen based the genus *Amazonia*, on *Meliola asterinoides* Henn. That these three genera, *Meliola*, *Amazonia* and *Asterina*, are without doubt very closely related to one another is shown by their development, and emphasized by this lack of uniformity in agreement with regard to the proper position for *Amazonia*.

The chief distinction between *Meliola* and *Asterina*, in the morphology of the ascocarp and exclusive of such details as spore character, lies in the fact that the development of the ascocarp in the former is by epinastic growth while in the latter the growth is hyponastic. In *Meliola*, though the ascocarp at its start is a flattened structure, on approaching maturity the upward development to accommodate the large asci in fasciculate arrangement results in a spherical fructification with an enveloping hood-like or flammeaceous stroma. In *Asterina* it is found that the nature of its growth causes a spreading of the basal portion and results in a flattened fruit with the asci in a broadened hymenium. As a consequence of this spreading of the fructification in *Asterina*, in close contact with the surface of the host, the stromatic cover is also spread and its margin, instead of folding under as in *Meliola*, is extended and exposed at all times thus forming a clypeate stroma.

Varying degrees of hyponasty may be followed through the Microthyriaceae to the extreme case in *Trichothyrium* where, due to an excessive growth of this sort, the margins of the discus-shaped ascocarps are turned upward from the substratum when mature. Instead of removing the Microthyriaceae, as has been suggested, to a position within the Discomycetes it would seem more natural to retain them among the Perisporiales, or at least rank them as an offshoot from that order. Their flattened form and the fact that their perithecia (thyriothecia and katothecia of von Höhnel, 1910, 1917) develop under a radiate stroma does not seem sufficient justification for the change. It also appears that the reduction which has taken place in the perithecial wall results in a seeming parallelism with the Dothideales, and is probably due to similar factors.

A thin heavy-walled stroma substitutes for the outer protective wall of the perithecium in a number of instances.

The presence of spermatia would seem to indicate that possibly Arnaud (1910) is justified in the removal of *Limacinia*, *Capnodium* and other related genera formerly placed in the Perisporiales to the Amphisphaeriaceae among the Sphaeriales. Here again it seems more practical to me, however, to retain them within the Perisporiales as an early branch from a point near where that order has its origin from the Sphaeriales, and as relatives of genera near *Parodiopsis*. Such a conclusion would justify Von Höhnel's erection of the family Capnodiaceae for their reception. Cytological investigation is needed in connection with these forms in order to fix definitely their exact position. From present indications it seems more probable that the presence of spermatia among certain genera of the lower Perisporiales should be considered indications of where divergence took place rather than warrant for their removal from that order.

Arnaud (1918, 1925) considers that the Dothideales and the Microthyriales are orders which have had a parallel development. In this later arrangement of his he places *Meliola* at the top of the Dothideaceous branch as dissociated and superficial rhizomophic forms. The Wardineae, including *Asterina*, he locates as the culmination of the Microthyriales. As he places the genera *Meliola* and *Asterina* each at the top of separate phylogenetic lines we must conclude that he considers these lines as approaching one another rather than developing in the usual manner of diverging ascent.

This removal of the *Meliolae* to the Dothideales cannot be accepted either on the basis of stromatic development or perithecial formation. They must be excluded from the Dothideales in the first case because their thin flammeaceous stroma has the totally different mode of development found among members of the Perisporiaceae and their relatives. In the second instance they are excluded because of the well developed ostiolate perithecium with protruding periphyses formed *under* the protection of this stroma. As at present restricted the Dothideales develop a plurilocular fructification. Though it is perfectly possible for a reduced stroma, and a consequent simplification of the fruit, to occur within this order, the Phyllacoraceae, where such tendencies appear, do not seem to offer a reasonable point of contact for a genus with the characteristics of *Meliola*. Further cytological study among the Perisporiales including more species of *Meliola* and related genera is much needed.

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Explanation of plates

All figures were drawn with the aid of the Abbe camera lucida. Figure 5 is drawn to a magnification scale of approximately ×640; all other figures to one of approximately ×1075.

PLATE 16

Fig. 1. Ascocarp anlage, end view in relation to leaf surface.

Fig. 2. The same as figure 1 but in side view; of approximately the same age.

Fig. 3. Young ascocarp in median section. The oögone appears in the center with its large fusion nucleus. From its basal cell two filaments of the investing hyphae which go to make up the perithecial wall can be seen, one on either side. The spirally twisted antherid appears beneath the oögone, while over all the hood-shaped stroma forms a complete protection.

Fig. 4. The ascogone shows a length of several cells with a branch beginning to develop from the penultimate. A stomatopodium appears at the entrance to the stomatal cavity and the whole growth is closely applied to the host cells.

Fig. 5. The core is continuing development beneath the stroma which has developed somewhat in thickness. The ascogone is heavy staining and appears near the center, while surrounding it appear cells partly ascogenous hyphal and partly perithecial.

Fig. 6. The ascocarp is assuming its spherical form, and the cells of the perithecial wall are clearly distinguishable within the stroma. The ascogenous hyphae fill the center.

Fig. 7. Normal epidermal and palisade cells of the host.

Fig. 8. The fungous filaments are closely applied to the surface of the heavily cutinized epidermis. This cutinized layer has been eroded, and the content of the epidermal cells shows that some injury has been sustained though no haustoria are present.

PLATE 17

Fig. 9. The young asci are seen to arise from the basal region of the ascocarp. A few scattered paraphyses are present and periphyses are developing in the upper portion of the cavity. The flattened perithecial cells can be distinguished from those forming the stromatic hood.

Fig. 10. Crozier formation is typical.

Fig. 11. A single crozier and two young asci with fusion nuclei.

Fig. 12. In each ascus four spores are cut out simultaneously, each contains two of the original eight nuclei.

Fig. 13. As two of the spores develop the other two degenerate and finally disappear.

Fig. 14. The mature ascus contains normally two five-celled spores. Their middle cell contains two nuclei, while the others have but one each. These nuclei arrange themselves on the side of the spore away from its neighbor.

Fig. 15. In the development of the spore the two original nuclei divide to form four, and a daughter of each moves toward the ends of the spore and the terminal cells are cut off. The two nuclei remaining in the center then divide and one nucleus from each will be located in the center cell of the spore.

Fig. 16. When mature the spore is heavy-walled and the content is barely discernible.

Fig. 17. The periphyses push their way between the cells of the stroma and the ostiole is formed at the top of the ascocarp, but not till late and when mature spores are present.
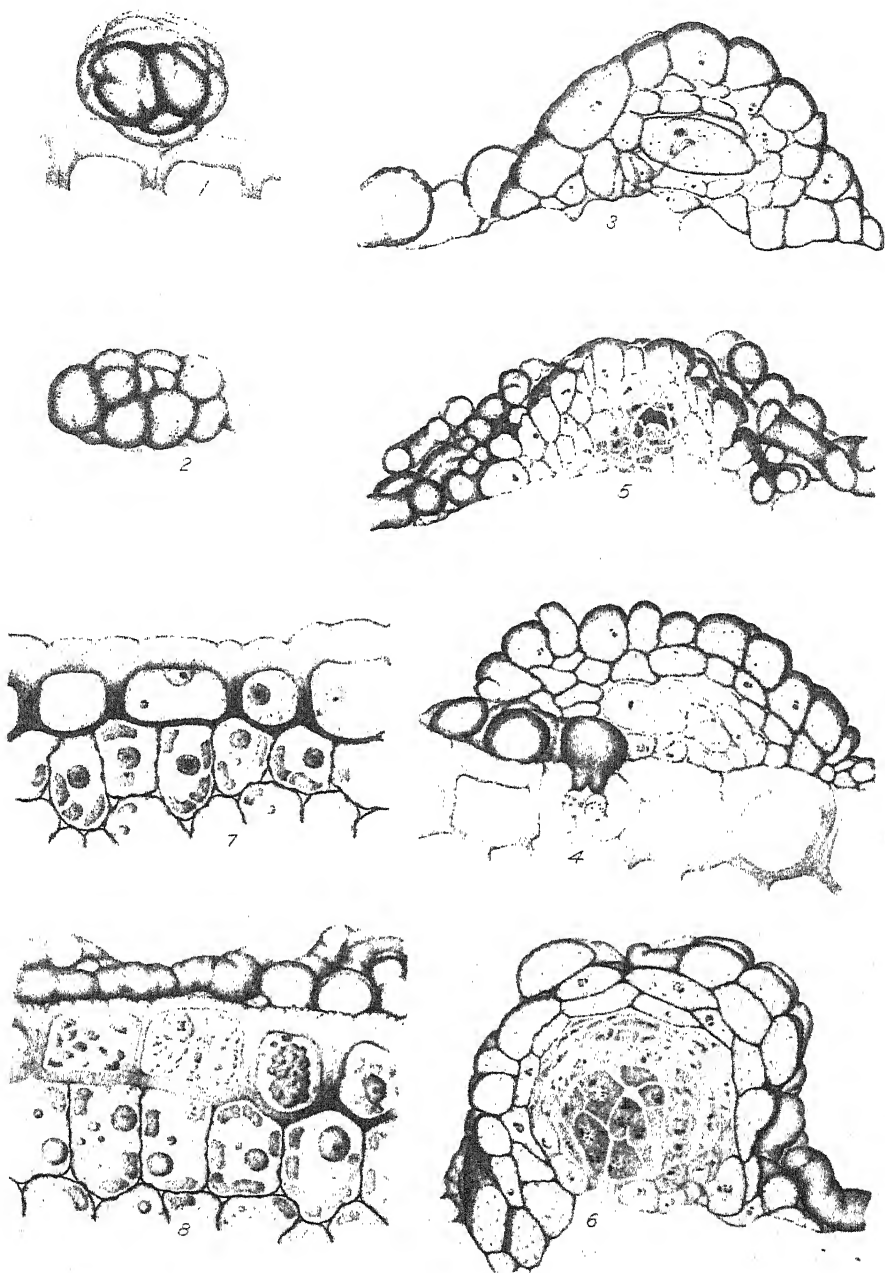
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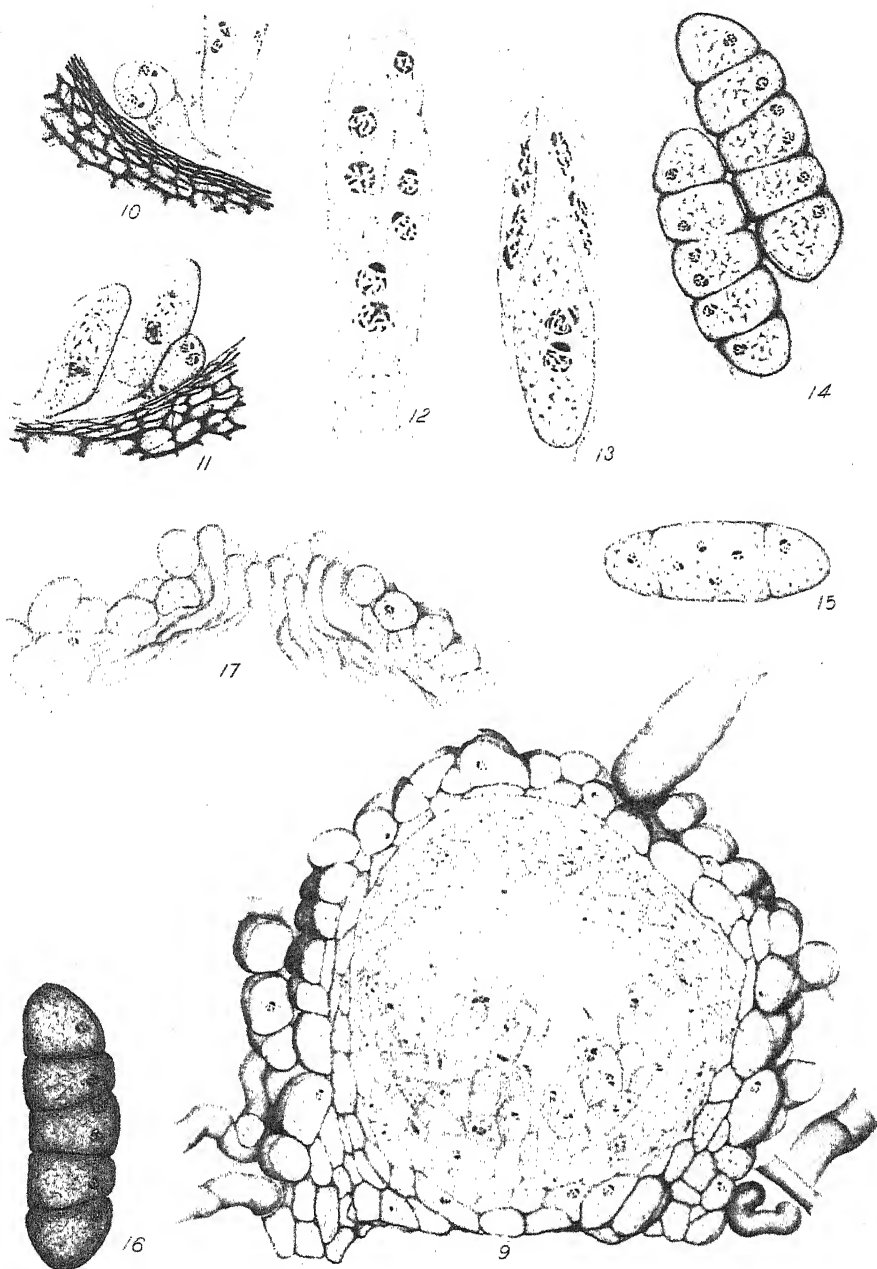
GRAFF: MELIOLA

A progeny study of the so-called oak species Quercus Saulii, with notes on other probable hybrids found in or near the District of Columbia

H. A. ALLARD

(WITH FOUR FIGURES)

FERTILIZATION PHENOMENA IN THE WHITE AND BLACK OAK GROUPS

Two distinct groups of oaks occur in the eastern United States, one known as the white oak group, the other known as the red or black oak group. So far as known all the American oaks of the white oak group mature their fruit the same year in which pollination takes place, making them annual fruited species. The species of the black oak group are dominantly biennial in the development of their fruit. Counting from the time of pollination all our Washington species belonging to this group require two years for the maturation of their fruit.

These contrasting behaviors probably rest upon fundamental physiological differences in the fertilization phenomena of the two groups at present not at all understood. When pollen reaches the stigma of members of the white oak group, the growth of the pollen tube containing the male cells follows an uninterrupted advance into the tissues of the style until the ovules are fertilized. In the case of the black oak group the typical biennial behavior occurs; the pollen falling upon the stigma begins its growth as in the white oaks, the pollen tubes invading the tissues of the styles until the stylopodium, which appears to be essentially the coherent basal portions of the three styles, is reached. For some unknown reason the pollen tube ceases further growth here during the current season of pollination, and appears to pass into a dormant or resting condition until the second spring, when fertilization of the ovules proceeds as in the annual fruited white oaks. In the case of the black oaks it would appear that the stylopodium is a sort of hibernaculum for the resting pollen tube. In some respects this is a most remarkable behavior and leads one to wonder if external environmental conditions may not modify this course of events, and perhaps allow the pollen tubes to make an uninterrupted advance into the ovules as in the case of the white oaks.

Several years ago while making studies of the effects of various lengths of day upon growth and reproduction in plants, the writer conceived the idea that perhaps a localized modification of the length of day upon the twigs and inflorescence of the willow oak *Quercus phellos* would disturb this distinctive cessation of growth and resulting dormancy of the pollen tube, and bring about an annual fruiting condition in the treated branches.

Accordingly, ventilated dark cases were so arranged on several trees at Arlington Farm, Virginia, that fruiting branches before anthesis could be subjected to ten hours of daylight only each day throughout the summer. These particular experiments were unsuccessful and the treated branches remained biennial in their fruiting behavior. Tests of a single season cannot be considered final, however, and it may be that experiments begun from the time of germination of the acorns, using various lengths of day would reveal an entirely different story for the initiation of the reproductive structures, and the subsequent annual or biennial behavior of the oaks. At the present time there is nothing to indicate why the pollen tubes of the black oaks should show the specific resting behavior in the stylopodium characteristic of their growth during the first season. The behavior still remains an enigma for future experimentation.

Natural pollinations are producing intra-specific hybrid forms now and then in the field, but so far as known, these hybrids in all instances are confined strictly to their own groups. It would seem that any white oak species in a locality can fertilize readily any other member of the white oak group. Likewise any black oak in a locality may, it would seem, quite as freely fertilize any other member of the black oak group.

These natural inclinations on the part of the oaks have given rise to quite an assemblage of intra-specific hybrids which have proven not only of much interest to botanists but a positive worry to systematists, bent upon an honest and helpful labeling of all plants in the field.

Even though in the case of the oaks wind pollination is the rule and the light wind-blown pollen is free to settle where it will, hybrid trees are always sporadic in their occurrence, and never common in any locality. In spite of the free intermingling of species everywhere, the purity of the various species is to be remarked upon rather than a positive, identifiable hybridity of the populations. As an offhand guess this would indicate, perhaps a self-prepotency for the oaks as has been found to exist in maize.

ALBA × MONTANA

Several oak hybrids are already listed in our District Flora, of which little is definitely known concerning their parentage. Among these is the so-called species *Quercus Saulii* Schneid, supposedly representing the hybrid *Q. montana* Willd. × *alba* L.

In 1883 George Vasey,[1] a Washington botanist, described and illustrated several oak hybrids recognized in the vicinity of the District of Columbia. One of these was Saul's Hybrid (*Q. Saulii*). Vasey's illustration

[1] VASEY, GEORGE. On three hybrid oaks near Washington, D. C. Bull. Torrey Club 10: 25–26. *pl. 28–30.* 1883.

of this oak shown in his plate 28 does not as well represent the leaf forms characteristic of individuals which I have found, as his plate 29, and perhaps plate 30. These two latter, however, he has considered to be hybrids of *Q. alba* with *Q. stellata.*

I have found several individuals of Saul's oak in the Washington region. A particularly fine large tree stands on Pershing Drive, near Maryland Avenue, Ashton Heights, Clarendon, Va. I have found other individuals near Chevy Chase Country Club. Almost at a glance one can detect evi-
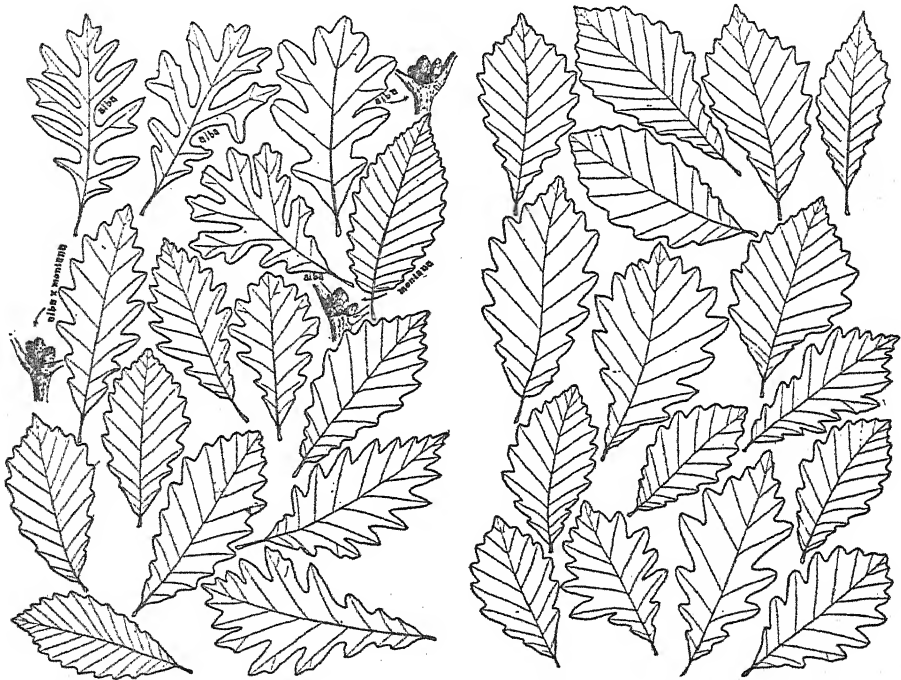
Fig. 1. Left. Leaves of *alba, montana* and leaves of the hybrid form *Saulii*, together with buds. *Montana* buds are shown near the petiole of the *montana* leaf. Right. Other leaves of the hybrid form *Q. Saulii.*

dences of *montana* blood in these forms, not only in the deeper even lobing of the leaves, but in the droop or hang of the foliage and in the size and shape of the acorns and the cup.

About ten years ago, I secured a quantity of acorns from the tree on Pershing Drive, and planted them in garden soil. About forty seedlings were obtained, the majority of which have been allowed to grow until the present time. Many of the individuals of this progeny have shown rapid yearly growth and the largest have now attained a height of 15 feet. A careful analysis of the progeny was made and a typical representative leaf

selected for illustration from each tree. At a glance it is seen that many intermediate forms have appeared, representing different degrees of approach to one or the other parent *montana* or *alba*. As a whole the progeny shows a dominance of *montana* characters, in the shallow, more numerous and uniform lobes of the leaves and the presence of more or less minute whitish pubescence beneath. However, there are individuals with larger and irregular lobing of the leaves, showing unmistakable white oak parentage.

With respect to the autumnal behavior of the individuals of this progeny, some striking features are shown. A number of trees show the more typical red-brown coloration of the *montana* parent; others show the more coppery red indicative of *alba* blood. Others have shown an almost entire dominance of yellow hues, giving evidence of little anthocyan in the leaves. One vigorous individual of particularly obvious *alba* stamp has assumed each year a most gorgeous, deep red coloration, such as I have rarely if ever seen equaled by any member of the white oak group. This particular tree likewise loses all its leaves promptly, behaving less like a typical white oak, and more like the chestnut oak in this respect. Another vigorous individual with a decided hybrid stamp approximating more closely the *montana* type of leaf, except that it is narrower and more elongate, assumes a deep red brown coloration each autumn, but the leaves show a decided tendency to cling to the branches as is the characteristic behavior of many *alba* trees.

With respect to autumnal coloration, leaf fall, etc. it is indicated that we are dealing with individual and hereditary features, which in their genetic behavior may show unit-character relationships such as obtain with leaf-form or any other feature of vegetative or reproductive expression.

When natural hybrid forms are found in the field, it is evident that we have no assurance as to what generation is actually involved, whether the original cross appeared in the F_1 generation or some subsequent generation descending from this. In the case of all fruit which I have obtained from *montana* $\times$ *alba* (*Saulii*) trees, the acorn and cup have been decidedly of the *montana* type.

To say the least, it is evident that the so-called oak species *Quercus Saulii* combines *montana* and *alba* blood. With greater numbers representing the progeny, it is possible that far greater extremes of variability may yet be found, with much closer approximations to the *alba* parent.

ABERRANT FORMS WHICH APPEAR TO REPRESENT HYBRIDS

Phellos $\times$ *marilandica*. A small tree found at Lyon Park in a colony of *Q. phellos*, *Q. marilandica* and other upland oaks. The leaves are very vari-

able in shape ranging from the unlobed type through forms slightly wavy-margined to more extreme forms. In some instances, one weak obtuse or rounded lateral lobe is present; in others a pair of lateral lobes of this type occurs. The more prominent lobes occur well toward the apex of the leaf. These as well as the apex of the leaf are conspicuously bristle-pointed. The leaves are thick and rather coarse in texture, with a somewhat wavy surface, and average around 4 to 4.5 inches long and 1.25 to 2 inches in width. The petiole is very short—only 1/8 to 3/16 inches in length. The undersurface is mostly smooth except for a whitish scattered pubescence along the midrib and in the vein axils. The color of the leaves is a rather deep green, deeper than that of *phellos*.
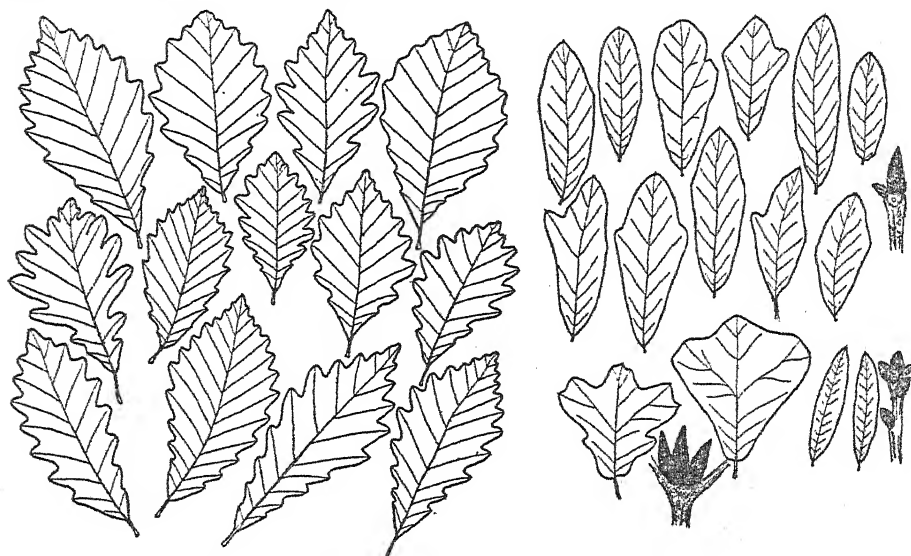
Fig. 2. Left. Additional leaves of the hybrid form *Q. Saulii*. Right. Top and middle row showing leaves and buds of supposedly hybrid form *phellos×marilandica*. Lowermost row, two leaves and buds of *marilandica* at left; two leaves and buds of *phellos* at right.

The buds are much more elongated and sharp pointed than in the case of the willow oak. This feature together with more pronounced pubescence of the bud scales and the more pubescent condition of the new twigs, affiliates the tree more closely with *marilandica*.

The very short stout petioles of the supposedly hybrid forms would suggest *marilandica* blood rather than *rubra* (*falcata*).

It is interesting to note in this connection that N. L. Britton[2] in 1882 was the first to describe a *phellos×marilandica* cross as he judged certain

[2] BRITTON, N. L. On a hybrid oak near Keyport, N. J. Bull. Torrey Club 9: 13–15. *pl. 10–12*. 1882.

oak trees to be occurring near Keyport, New Jersey, giving it the specific designation *Quercus Rudkini*. Britton illustrated his paper with several color plates of leaves of his supposed hybrid. In form these very closely resemble the leaves of my own tree. C. S. Sargent[3] in 1895 illustrated the supposed cross of *phellos* × *marilandica*, which, like Britton's illustrations, agree closely with my own material.

In 1907, D. T. MacDougal[4] made progeny studies of this oak named *Q. Rudkini*, securing about 100 seedlings from planted acorns. While he found much variability in the progeny he concluded that this was not
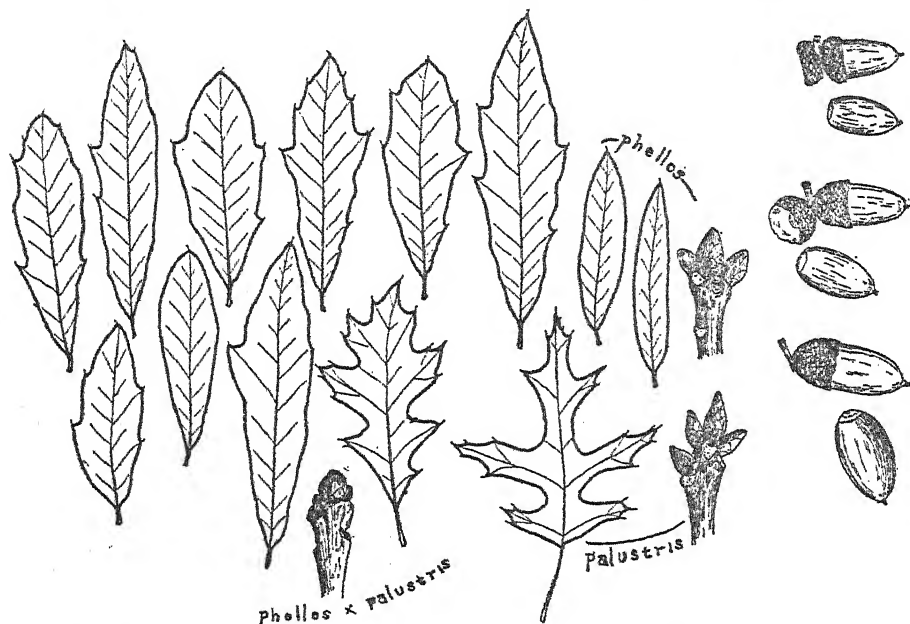
Fig. 3. Left and center. Leaves and buds of the supposedly hybrid form *palustris* × *phellos* and of the parent forms *phellos* and *palustris*. Right (above) Acorns of *alba;* (middle) *Saulii;* (below) *montana*.

more extreme than actually occurs in good oak species with a unified heredity. His final conclusion was that there was little in his progeny analysis to indicate actual hybridization, and that *Q. Rudkini* must be regarded as a good species until further studies disproved its taxonomic standing.

In this connection it may be said that the oaks found by Britton could still have a hybrid origin, and yet show a reasonable degree of variation in

[3] SARGENT, C. S. The silva of North America. **8**: *pl. 437.* 1895.

[4] MACDOUGAL, D. T. Hybridization of wild plants. Bot. Gaz. **43**: 45–58. *f. 1–4.* 1907.

the progeny as indicated by MacDougal. If a hybrid form appears, no one knows what generation is involved, and the trees in question may have been many generations removed from the original cross. A thousand trees would probably show greater extremes of variation than one hundred trees if a cross were involved.

Phellos × palustris. Young trees supposedly representing this cross have been planted on Pershing Drive continued, just east of Glebe Road. A considerable number of willow oak trees have been planted in this subdivision, two of which show leafage suggesting hybrid parentage. The oblong-lanceolate leaves are very variable in shape, ranging from forms with entire margins to those with rather shallow lobes or mere bristle-pointed teeth. Their average length is 4 to 4½ inches by 1 to 1½ inches wide. The petiole is very short and rather stout, averaging ⅜ inch long or less. The glabrous leaf-blade is bright green in color; in autumn the midrib and petiole assuming a deep crimson shade, which may even extend to the leaf blade. It is obvious that these oaks do not represent either the *phellos* type or the *palustris* type. The presence of teeth and lobes, the autumnal coloration and the general shape of the tree suggests *palustris* parentage. The very short petioles, however, are quite unlike the slender, flexible petioles of *palustris*, which are usually 1¼ inches in length.

Imbricaria × marilandica. In 1930 several young trees were found in the woods near the head of Pimmit Run which give indications of being hybrid forms. In the immediate locality trees of *imbricaria* and *marilandica* were growing, and in so far as circumstantial evidence can reveal the truth on the basis of parental resemblances, it would appear that these two species have been involved in the supposed cross.

In general shape the leaves are oblong-lanceolate, 7 to 9 inches long, and 1½ to 3½ inches in width. The petiole is about ¾ to 1 inch long and rather slender. There is great variability of leaf-form on the same tree, the leaves varying from entire to slightly sinuate lobed, or with a pair of bristle-pointed lobes near the apex. The undersurface of the leaves is uniformly fine whitish puberulent. The buds are more elongate and acute than in the case of *imbricaria*, but like this species nearly smooth as are the twigs below. The autumnal coloration assumed by the leaves in some instances was a most gorgeous deep crimson. While it is possible *rubra* (*falcata*) parentage could be involved, the general appearance of the leaves and the deep red coloration indicate *marilandica* affiliations rather than *rubra* (*falcata*).

In 1877 George Engelmann[5] reported finding a tree near St. Louis in

[5] ENGELMANN, G. About the oaks of the United States. Trans. St. Louis Acad. Sci. **3**: 372–400; 539–543. 1868–1877.

1849 which he regarded as a cross between *imbricaria* and *marilandica*. The leaves appeared to be those of the former with a hint of the peculiar lobing of *marilandica*, being coarsely 3-dentate at the apex, or with a few teeth on the sides. In some instances the leaves were entire.

C. S. Sargent[6] in 1895 illustrated material supposedly derived from this cross *imbricaria* × *marilandica*, which bears a striking resemblance to my own material.

Bartram's Oak, *Q. heterophylla* Michaux (*phellos* L. × *maxima* (Marsh.) Ashe). This is an uncommon form in the District Flora, although I have been fortunate enough to find material of this botanically historic species. No oak in our American flora has acquired the romance of botanical interest that this oak has inspired since the younger Michaux described it as a new species in 1810. A long line of the foremost botanists of America as well as many others of less distinguished note have ventured their opinions considering the origin and affiliations of this historic form. Some have vouched for its hybrid origin; others have as dogmatically affirmed against such a possibility.

L. S. Gale,[7] writing in 1855, was most strenuously opposed to such an origin, and even went so far as to deny all hybridization among oak species. It may be stated here, however, in due respect to the rather decided opinions of Gale that he appears to have made some of the first sincere efforts to unravel experimentally the heredity of the Bartram Oak. Gray in 1848 considered it a possible cross between *phellos* and *falcata*. From 1851 to 1855 Gale planted acorns of the Bartram Oak which he discovered in Washington. Seedlings which he secured resembled the parental form closely. At the same time he attempted to hybridize by careful control methods of bagging with cloth balloons, as he called them, *falcata* with *phellos* and the Bartram form. As a result of his first pollination experiments in 1852, acorns were obtained from *phellos* pollinated with *falcata*, and *falcata* pollinated with *phellos* pollen. It is evident that Gale was even expecting a direct effect of the pollen upon his crossed acorns, for he remarked that the acorns always resembled the mother parent. When the planted acorns gave rise to seedlings there appeared to be no observable difference between the seedlings arising from the bagged acorns and those unbagged from the same trees. It is here that Gale was wrong, for the Mendelian behaviors of crosses had not at that time enlightened the botanical world. Today we know that the F_1 plants may have been strikingly like one of the parents, and that the breaking up of a dominant or a

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[6] SARGENT, C. S. Op. cit., Plate 433. (See footnote 3.)

[7] GALE, L. D. On the oaks of the District of Columbia. Proc. of the Nat. Inst. Washington, 1: 67–77. *f. 1, 2.* 1856.

blended F_1 uniformity would become evident in later generations. In the spring of 1854 Gale carried out similar pollination experiments, using more closely woven bags, and secured no acorns whatever.

It would appear that the Bartram form described by Gale was the second positive discovery of a Bartram Oak. About the year 1855, trees of a similar type were found at Mt. Holly, New Jersey, and subsequently at various other stations in New Jersey, Delaware and Staten Island, New York, and the range of the form has now gradually extended well into the South. Opinions of botanists that had centered of necessity around the
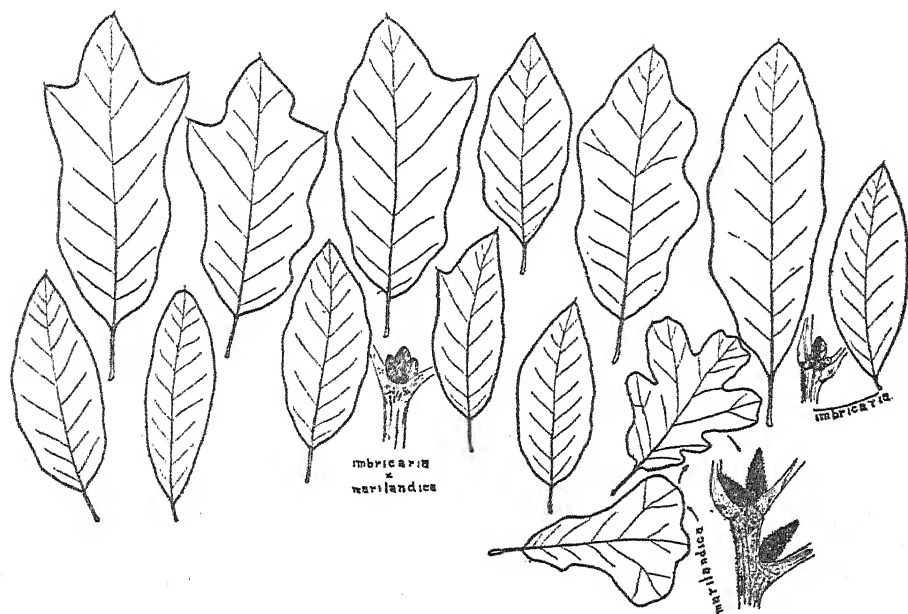
Fig. 4. Leaves and buds of the supposedly hybrid form *imbricaria* × *marilandica*. At extreme right a leaf and buds of *imbricaria* are shown. Buds below and two adjacent leaves at left represent *marilandica*. Remaining illustrations represent the suspected hybrid.

single original specimen of Michaux, until about 1850, were now directed to a group of sporadic occurrence. At one time or another, nearly every deep-lobed member of the black oak group has been considered one of the parents in a *phellos* combination, including *rubra* (*falcata*), *coccinea*, *palustris* and *velutina*. Strangely enough, *maxima* (Marsh.) Ashe, had never been mentioned.

In 1888, as a result of his studies of forms resembling the Bartram Oak found at Tottenville, Staten Island, New York, Arthur Hollick[8] finally

[8] HOLLICK, ARTHUR. A recent discovery of hybrid oaks on Staten Island. Bull. Torrey Club 15: 303–309. *pl. 83–85.*

concluded that this oak is the result of the cross *phellos×rubra* (*maxima*) as the northern red oak is now designated. This original opinion is of some interest, in the light of a careful progeny analysis made by D. T. McDougal[9] in 1907. A progeny of 55 seedlings obtained from acorns of a Bartram form gave a range of variation extending from *phellos* to *maxima*. As a result of his analysis, MacDougal concluded that Bartram's oak is an indubitable hybrid which has arisen between *phellos* and *maxima*.

This would seem to establish fairly accurately the status of the puzzling Bartram Oak, and withdraw it from the *phellos×velutina* parentage which has been ascribed to it in the "Flora of the District of Columbia and Vicinity," Contr. U. S. Nat. Herb., Vol. 21, 1–329. 1919.

Imbricaria×velutina (*Q. leana* Nuttall) is an uncommon form in the District of Columbia.

Alba×stellata has also been reported in the *District Flora*, and has been variously figured.

It is evident that the District of Columbia embracing an area of no large size offers rather interesting opportunities for the study of hybrid oak forms. As a matter of fact this limited area is especially rich in oaks, 14 undoubted species being listed in the *District Flora*, one, *ilicifolia*, of less certain occurrence, together with four presumably hybrid forms.

In this connection it is interesting to note that at the time Gale was writing in 1855, *Q. imbricaria* was not considered indigenous to the District, and even *Q. rubra* (*maxima*) and *Q. bicolor* were considered extremely rare. As a matter of fact Gale reported that he added *rubra* for the first time to the District flora, which had not been reported in the Flora Columbiana of John A. Brereton, published in 1830. Gale found a single tree on the banks of Rock Creek in a cool shaded ravine, and thought this was the sole representative of a northern species. He was the first to record Bartram's oak in the District of Columbia on his own statement. In 1855 the chestnut oaks *prinoides, prinus,* and *Muhlenbergii* appear not to have been reported in the District assemblage of oak species.

It would seem that nature is producing rather rarely and sporadically hybrid forms. This suggests that a most attractive problem awaits some young, hopeful school of field botanists interested in further studies of of natural hybrid forms, as well as in the experimental production of new hybrids. A study of such hybrid progenies beside the parental seedlings would quickly reveal to what degree hybrid vigor may obtain, and settle many little nomenclatorial troubles in the *Quercus* assemblage.

In every locality there is an urgent need for a careful recording of all

[9] MacDougal, D. T. Op. cit. (See footnote 4.)

hybrid or anomalous forms in order that they may be preserved whenever possible, or at least kept from utter extinction in their progenies. These rare and sporadic incidents of nature are too interesting and beautiful to treat with indifference, with a flora being woefully mistreated and reduced to pitiful remnants in many sections. It would be well if parks or arboretums could be maintained in the Washington region where anomalous or hybrid forms could find a home for future botanical studies.

In spite of the sporadic occurrence of hybrid forms let no one think it is an easy matter to give readily every oak tree to be met with an indisputable specific label, for many categories of variation more or less local or regional obtain for every species in the field. In the past, unfortunately, the tendency has been shown to give specific names rather freely to every unusual form or supposed hybrid encountered in the field. In more than one instance the result has been to clutter the nomenclature of the oaks with many species names which really have no good standing as representing distinct species composing the facies of the flora of a region. Surely the species concept must carry with it some attention to the progeny constancy of a form, either as determined by the general resemblances of a natural assemblage in the field, or by actual progeny studies. Many of our listed hybrid species would unquestionably show a most bewildering array of intermediate forms and perchance parental reversions if their progenies were intensively analyzed, as in the case of the Bartram Oak. If it is legitimate taxonomic spirit to name in turn these varied assortments representing all manner of combinations of leaf and fruit characters which are certain to occur in hybrid progenies, a world of intergrading oak species is yet to be listed by zealous students of oak hybrids. Such a viewpoint, however, could only result in hopeless confusion for the naturalist.

Bureau Plant Industry
Washington, D. C.

Useful plants of Yucatan

ROLAND M. HARPER

Most of Mexico is rather mountainous, with great variations in rocks and minerals, soil, climate and vegetation in comparatively short distances. But the peninsula of Yucatan, comprising the states of Campeche and Yucatan and the territory of Quintana Roo, with a combined area of about 55,000 square miles, differs markedly from the rest of the country in being a plain of horizontally bedded late Tertiary limestones, broken by a few low ridges, and rising gradually to an elevation of some 900 feet at a distance of 100 miles from the coast. There are practically no surface streams, the water circulating in subterranean channels in the limestone, with many natural well-like openings of various sizes, known as *cenotes*, affording an unfailing water supply for the former and present inhabitants. Being within the tropics, the climate is always warm. The northern coast is rather dry, but farther south the rainfall is ample, and most of it comes in summer, as in southern Florida, which resembles Yucatan also in many of its features of geology, topography and vegetation. (And indeed Key West, Florida, is nearer to the northeastern corner of Yucatan than it is to Jacksonville.)[1]

Yucatan is noted among archaeologists the world over for having been the home of the Mayas, whose temples and inscriptions, hewn from the native limestone, show them to have had the highest civilization in the western hemisphere about a thousand years ago. This civilization had already begun to decline before the Spanish invaders arrived, however, for reasons not fully understood, and the Maya Indians who inhabit the wilder parts of the peninsula today are little better than savages.

The fish and game resources of Yucatan must have been inferior to those available to the North American aborigines, and the Mayas, who had little commerce with other peoples, must have lived mainly on vege-

[1] There is a vast amount of literature on Yucatan, largely archaeological. Besides the volume on which the present paper is based, and other botanical literature referred to in it, the following reasonably accessible works will give a pretty good idea of the natural conditions there.

Leon. J. Cole. The caverns and people of northern Yucatan. Bull. Am. Geog. Soc. **42**: 321–336. *f. 1–14*. May, 1910.

Ellsworth Huntington. The peninsula of Yucatan. Bull. Am. Geog. Soc. **44**: 801–822. *f. 1–11*. Nov. 1912.

See also H. H. Bartlett, A biological survey of the Maya area. Bull. Torrey Club **59**: 7–20. 1932.

table products. During the centuries that they lived there, they must have found uses for a large proportion of the native plants; and their plant lore has been passed on pretty well to the present inhabitants, both aboriginal and Caucasian. They had a few important cultivated plants which originated in America even if they were not indigenous to Yucatan, such as cotton, corn, beans, and sweet potatoes.

In modern times the exports from Yucatan have been almost entirely vegetable products, for the only mineral resource, limestone, is common in most other countries, animal products are unimportant, and there are no manufactures to speak of. Exports of logwood and mahogany from the peninsula are said to have begun two centuries ago or more. The most important forest product at present is chicle gum, but that is surpassed in value by henequen fiber (also known as sisal), derived from cultivated plants of American origin.

Existing knowledge of the plants of the peninsula has been brought together in convenient form in Paul C. Standley's recent Flora of Yucatan.[2] It happens that the author had never been in Yucatan, but he had been in other parts of Mexico, and in Central America, and a few years ago he published a voluminous work on the Trees and Shrubs of Mexico.[3] In the Yucatan flora all the plants, both wild and cultivated, about 1250 species, known to occur in the peninsula, are listed, with copious notes on Maya and Spanish names, uses, etc. The chief source of information was the work of Dr. George F. Gaumer, a physician and amateur botanist, who lived in Yucatan from 1885 to his death in 1929. Another important contributor was Dr. Charles F. Millspaugh, who was also a physician before he was a botanist. He visited the peninsula and neighboring islands in 1894 and 1899, and spent much time during the remainder of his life in studying at the Field Museum the collections made by himself, Gaumer and others. Several other botanists who either visited Yucatan or described plants from there are mentioned in the bibliography, which covers nearly ten pages of Standley's work. Even yet, according to Mr. Standley, the flora is imperfectly known, especially that of the southern part of the peninsula, which is difficult to explore on account of the dense forests, the savage inhabitants, and the danger of malaria and other tropical diseases.

But enough is already known to show that the area contains a remarkable number of useful plants, especially medicinal ones. The information about medicinal plants may be more complete than usual, on ac-

[2] Field Museum, Bot. Series, 3: 155–492. (Publication 279.) Sept. 1930. Reviewed in Tropical Woods (New Haven) 24: 31–35. Dec. 1930.
[3] Contr. U. S. Nat. Herb., vol. 23. 5 parts, 1721 pp. 1920–1926.

count of the medical interests of Drs. Gaumer and Millspaugh, but such plants seem to be rather partial to limestone regions anyway.[4]

Standley's Flora of Yucatan will of course be frequently consulted by persons interested in tropical American plants, but those who merely look up the references to various species will not get the whole story. On account of the large number of economic plants mentioned in it, and the full notes on them, it has seemed worth while to the writer (who has never been any nearer to Yucatan than Key West) to pick out such plants from the text and group them by uses; which was a rather tedious task, but makes an interesting story. It would take too much space to mention them individually, and the names of most of them might be unfamiliar to most readers of the Bulletin; but that might be done for local consumption at some future time when the region is more thickly settled and the flora better known. For the present the approximate number of species in each large economic group will be indicated, and some of special interest mentioned, while in the smaller groups most or all of the species may be referred to. Cultivated plants of Old World origin enumerated by Standley will not be considered here, however, for those could be grown in any other region of similar climate just as well.

In Yucatan, as in most other tropical countries, woody plants constitute the bulk of the vegetation, and they are also more numerous in species than they are in cooler climates. Of all the native plants listed by Standley, 172 may be classed as trees, 226 shrubs, 71 woody vines, and 467 herbs; though of course there are many intermediate forms, and no two

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[4] See Torreya **30**: 75. June 1930.

Since this manuscript was sent to the editor—and therefore too late to be thoroughly digested now—the Department of Middle American Research of Tulane University has published a 359-page bulletin or volume entitled *The ethno-botany of the Maya*, by Ralph L. Roys. (Middle American Research Series, Publication no. 2. August, 1931.) It was nearly all written before the publication of Standley's Flora of Yucatan, but the author corresponded with Standley, and utilized some of his material in manuscript form.

A catalogue of symptoms, with the plants prescribed for them, and copious quotations and translations from Maya texts, occupies over 200 pages, and an annotated alphabetical list of Maya plant names, with their scientific equivalents and therapeutic uses, over 100 pages. (A similar but more condensed list of animals occupies 17 pages.) An index of botanical names includes over 600 entries, exclusive of synonyms, but no page numbers. However, the Maya equivalents are given, and can be looked up in the alphabetical list.

Little is said about plants used for other purposes than medicine, except in a six-page chapter on the climate and food supply of Yucatan, near the end. A bibliography, with many of the citations incomplete as to page numbers, and including much relatively inaccessible manuscript material, occupies the last eight pages.

persons would count them in the same way. The useful plants are distributed in about the same proportions.

SHADE TREES AND ORNAMENTALS

The only native plants specially noted as used for shade trees are *Achras Zapota* (which is useful in several other ways, as noted farther on), and *Gliricidia sepium*, a small leguminous tree called *zacyab* by the Mayas and *madre de cacao* by the Spaniards. The latter name refers to its use for shade in cacao plantations in Mexico and Central America, just as some other trees are used to shade coffee.

Many plants are mentioned as being handsome when in bloom, but the number of natives cultivated for ornament apparently does not exceed a dozen, if Mr. Standley's information was reasonably complete. Among these are *Mirabilis Jalapa* and *Dahlia variabilis*, familiar in American gardens, which are believed to have originated somewhere in Mexico, but not in Yucatan.

Two small trees, *Jatropha Curcas* (Euphorbiaceae) and *Spondias purpurea* (Anacardiaceae) are said to be often planted for living fence-posts. Two large shrubs, *Urera baccifera* (Urticaceae) and *Pedilanthus itzaeus* (Euphorbiaceae), are used for hedges, and some of the cacti may be used in a similar way, as they are elsewhere in Mexico.

TIMBER TREES

In the first two parts of Standley's Trees and Shrubs of Mexico 26 species of *Pinus* and 112 of *Quercus* are listed, and the supplement in the last part adds 145 more of *Quercus*.[5] But neither pines nor oaks are definitely known in Yucatan, though Standley mentions rumors of a pine on ridges in the extreme south, which is probably *P. Caribaea*, the same species that is characteristic of southern Florida, western Cuba, and British Honduras. And if that region were better known some species of *Quercus* might be found there too, as there are a few in Cuba and Central America. However, even without pines and oaks, Yucatan does not lack timber. About twenty species of trees are reported by Standley as used in the construction of buildings, and about one-third of these belong to the families formerly included in Leguminosae, which are largely represented in tropical forests all around the world. One or two others are used for

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[5] Nearly all these supposed additional species of *Quercus* were described by Trelease in 1924. Apparently *Quercus* in Mexico has been having a "boom," like that of *Crataegus* in the United States a generation ago. (See Geol. Surv. Ala., Monog. 9: 203–208. 1928.)

posts and poles, and about a dozen trees that are too small or rare or hard for ordinary lumber are used for cabinet-making and similar purposes. Mahogany, one of the best of all cabinet woods, was formerly an important export.

FIBER PLANTS

Several tough woody vines, belonging to the genera *Paullinia* (Sapindaceae), *Arrabidea*, *Cydista* and *Pithecoctenium* (the last three Bignoniaceae) are used like ropes for binding the poles of roofs, walls or fences together, and coarse ropes and twine are made from the bark of such small trees and shrubs as *Bauhinia*, *Abutilon*, *Hibiscus*, *Hampea*, and *Guazuma*, most of these belonging to the Malvaceae and allied families.

Baskets, mats, thatched roofs, or brooms are made from *Typha angustifolia*, two sedges, two palms, and two shrubs of the genus *Acalypha*, which is represented in the eastern United States by a few weeds.

A malvaceous weed, *Sida acuta* (common also in Florida, where there are a few related species with similar properties), yields a strong bast fiber formerly used for making hammocks. Sea-island cotton, of the same family, was cultivated by the Mayas in pre-Columbian times, and has been exported, especially during our Civil War, but is now grown only for home consumption. *Ananas Magdalenae*, a near relative of the pineapple, is an important fiber plant, not certainly known in the Yucatan peninsula, but believed to occur in the southern part, as it does in Guatemala, not far away.

The most important export from Yucatan at the present time is henequen or sisal, a fiber from the leaves of two or three species of *Agave*, whose classification is still a little uncertain. Standley lists 170 species of *Agave* in the first part of his *Trees and Shrubs of Mexico* (though they are not what one would ordinarily call trees or shrubs), and 17 more in the supplement. Some of them are ornamental, some yield beverages, and some fibers; and some have been cultivated so long that they have developed varieties that cannot be assigned to any native home. Henequen was known and used by the ancient Mayas (who had several different names for it), and had already been transplanted to the Old World before the botanists classified it; and some of the species were originally described from plants cultivated in Europe, which complicates matters still further. From this fiber is made nearly all the binder twine used by the wheat growers of the United States and other countries. It is now grown in vast plantations in the drier and more accessible northern parts of Yucatan, and it brought considerable wealth to the state about the time of the World War; but since then the competition of Java and East Africa has

hurt the business.[6] The fibers of different species of *Agave* differ in quality, and there are differences of opinion as to which is the best; the British preferring that raised in their colonies.

Short fibers from the heads of cat-tails, from the trunks of the thatch-palm (apparently the same species as on the Florida Keys), and from the seeds of *Clematis dioica* and two species of *Ceiba* (Bombacaceae) are used for stuffing pillows, cushions, etc.

DECORATIONS

The red and black seeds of two leguminous vines, *Abrus precatorius* and *Rhynchosia pyramidalis*, are used for necklaces. The corollas of two species of *Jacquinia* (Theophrastaceae) and of *Plumeria alba* (Apocynaceae) are strung on cords for decorations for festal occasions.

FORAGE PLANTS

The principal wild forage plants are five or six coarse grasses (quite unlike the lawn and pasture grasses of temperate regions), *Viguiera helianthoides*, a coarse herb of the Compositae, the leaves and twigs of *Brosimum Alicastrum* (breadnut or wild cherry, of the Moraceae) and *Aeschynomene fascicularis* (a leguminous shrub), and the pods of *Prosopis Chilensis*, which is congeneric with the mesquite of Texas and adjoining states.

HUMAN FOODS

Plants used for human food are so numerous that they may well be subdivided according to the parts used. There are two important root crops, the cassava and sweet potato, which are certainly American, but have been cultivated so long that their exact origin is unknown. Of the former (genus *Manihot*, family Euphorbiaceae) Standley lists four species from Yucatan. The first two are wild plants of no importance, though one of them, *M. Carthaginensis*, or what passes for it, is a small tree now cultivated in Florida for ornament or as an oddity. *M. dulcis*, the sweet cassava, said to be non-poisonous, is used both as a vegetable and as a source of starch. *M. esculenta*, which is poisonous until cooked, but widely used in tropical America, is said to be native of Brazil, but is believed to have been brought to Mexico before the Spanish conquest.

Other "vegetables" are the young inflorescences of *Chamaedorea gram-*

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[6] The population of the state of Yucatan increased 5.8% between 1910 and 1921, while the rest of Mexico lost population; but the increase between 1921 and 1930 was only 7.3%, as compared with 14.4% in the whole country. Its capital city, Merida, ranks about fifth among the cities of Mexico in number of inhabitants, and is said to be very modern in appearance.

inifolia, a small palm, the young leaves of *Jatropha aconitifolia*, a small tree of the Euphorbiaceae, and the young fruits and ripe seeds of *Ceiba aesculifolia*, which is one of the large trees.

Wild edible fruits, either eaten raw or made into preserves, or both, come from about 12 large trees, 20 small trees, 2 woody vines, 5 shrubs and 6 herbs, which it would take too much space to list separately.

The most important seed eaten is *Zea Mays*, Indian corn, which has been cultivated so long that its origin is unknown, and it is no longer found wild anywhere. The Mayas had many different names for forms and parts of the plant and products derived from it. Standley says: "Upon the maize plant is based the whole Maya civilization. Exhaustion of the soil consequent upon the growing of the plant is believed to have caused the successive migrations."[7]

Two or three species of beans were known to the Mayas, and the same ones are now commonly cultivated in the United States; but, as in the case of the corn, their origin is unknown.

The cocoanut is common along the coast, as in all tropical countries, but it is believed to have been introduced by the Spaniards, as there is no Maya word for it.[8] Four or five other wild trees yield seeds that are eaten.

Beverages are made from the bark of *Lonchocarpus longistylus*, a leguminous tree, and from the seeds of one or two species of *Theobroma*, the cacao or chocolate tree.

Honey comes from the flowers of three trees, three shrubs and two herbs specially mentioned by Standley, and doubtless from many other species.

Flavoring materials and condiments are obtained from *Vanilla fragrans* (native in tropical America, but now cultivated mostly in the Old World), *Piper auritum* and perhaps others of that genus, *Pimenta officinalis* (allspice, of the Myrtaceae), *Capsicum annuum*, and a few other native plants.

MEDICINAL AND POISONOUS PLANTS

Among medicinal plants there are all gradations between important ones that have obtained world-wide recognition, and those whose virtues

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[7] Although corn is believed to have originated in Mexico or some other warm country, most of the American crop is now grown in the northern half of the United States. It is seldom seen in southern Florida, but that may be partly because it is attacked there by pests that were unknown in the time of the Mayas, and partly because present economic conditions make it more profitable for that part of Florida to raise tropical and semi-tropical fruits and early vegetables, which bring a much higher return per acre.

[8] For a recent and easily accessible account of the history of the cocoanut see J. K. Small, Jour. N. Y. Bot. Gard. 30: 153–161, 194–203. 1929.

are doubtful or imaginary. Every civilized country has its own pharma-copoeia, which naturally gives preference to its own products, especially when a local and a foreign drug have similar properties. A drug map of the world by Dr. E. L. Newcomb, published in 1929,[9] shows the principal sources of about 225 vegetable drugs. Of these about 100 are credited to the United States, and only 13 to the whole of Mexico and Central America. But in Standley's Flora of Yucatan about 150 wild plants (counting groups of two or more closely related species as one) are said to have medicinal properties; and one might venture the guess that at least half of those have some real value.

Drugs of more or less importance are yielded by 15 large trees, 36 small trees, 8 woody vines, 20 shrubs, and 75 herbs. Among the most important are *Myroxylon Pereirae* (balsam of Peru), *Guaiacum sanctum* (lignum vitae), *Asclepias Curassavica* (milkweed), *Capsicum annuum* (red pepper), *Chenopodium ambrosioides* (wormseed), and *Datura* spp. (stramonium). In temperate regions more medicines come from roots and tubers than from the above-ground parts of plants, but in the tropics bark, leaves, flowers and seeds are used more. In Yucatan, as in the tropics generally, there seem to be more drug plants in the Leguminosae than in any other family.

In connection with drugs, poisonous plants deserve mention, though some of course are anything but useful. Those whose sap is poisonous to the skin are *Hippomane Mancinella* (manchineel), *Hura crepitans* (sand-box tree), *Gymnanthes lucida* (these three all in the Euphorbiaceae), and *Metopium Brownei* (Anacardiaceae).

Internal poisons include the roots of *Zamia furfuracea* (camotillo)[10] and *Manihot esculenta* (cassava), and the seeds of *Abrus*, *Erythrina*, and *Karwinskia*. Curiously enough, the roots of both *Zamia* and *Manihot* contain an abundance of starch, and are used for food after the poison is destroyed by heat.

Gliricidia sepium, a small leguminous tree, is sometimes used for

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[9] See Torreya **30**: 74–77. June, 1930.

[10] The identity of camotillo seems to have been somewhat of a mystery. Standley does not give this common name in his Flora of Yucatan, but he does in his Flora of the Lancetilla Valley, Honduras, published a few months later. (Field Mus. Publ. 283, pp. 84–85. Jan., 1931.) Dr. Ralph H. Cheney, in recent papers on arrow-poisons (Sci. Monthly **23**: 554, 1926; Am. Jour. Bot. **18**: 138, 139, 1931) mentions camotillo as a plant reputed to be deadly, but does not identify it botanically. A recent newspaper syndicate feature mentions a Brazilian plant that is said to cause instant death to any one who touches it, and the picture accompanying it shows a plant which may very well be a *Zamia*. But the story is of course greatly exaggerated, for otherwise no botanist who attempted to classify the plant would have lived to complete his description.

poisoning rats and mice (whence its generic name), and two trees, *Pis-cidia* and *Hura*, and a woody vine, *Paullinia Cururu* (and related species) for poisoning fish.[11]

About half a dozen species of small trees, vines and herbs, of various families (especially Euphorbiaceae), are armed with nettle-like stinging hairs. The unwary explorer may get a dose of formic acid in another way, from two species of *Acacia* with hollow thorns, and species of *Cecropia* and *Cordia* with hollow twigs, which are inhabited by ants that rush out to attack anything that brushes against the plants or tries to climb them. Many similar cases (known as myrmecophilous plants) are known in other tropical countries.

CHICLE GUM

Achras Zapota is one of the most abundant and useful large trees in Yucatan. It is planted for shade, its wood is useful for many purposes, it is cultivated (in Florida as well as in the tropics) for its edible fruit (sapo-dilla), and it is the source of chicle gum of which hundreds of tons are exported from Quintana Roo every year. The gum was known to the ancient Mayas, but its use in chewing gum in the United States is a comparatively recent development. It is gathered chiefly by the Maya Indians in the dense forests in the southeast, by primitive and wasteful methods, and the supply is said to be already seriously depleted.[12]

DYES

Dyes come from about eight species, mostly trees and shrubs, and also from the cochineal insect, which feeds on a cultivated cactus. The most important dye wood is *Haematoxylum Campechianum*, the logwood, a small crooked leguminous tree. It was an important article of commerce as early as the 16th century, but has now been partly supplanted by aniline dyes. It also has astringent properties, recognized in the U. S. Pharma-copoeia. *Chlorophora tinctoria*, a small tree of the Moraceae, is the fustic of commerce, and yields yellow, brown and green dyes, which are used for dyeing khaki cloth.

OTHER PRODUCTS

Other products of a chemical nature from wild plants are charcoal from *Gymnopodium antigonoides*, a small tree or shrub of the Polygonaceae, rub-

[11] For a recent study of mymecophilous plants, mostly from northern South America, see H. A. Gleason. The relationships of certain mymecophilous melastomes. Bull. Torrey Club **58**: 73–85. 1931.

[12] The process of gathering it is described in detail in an account copied from an English publication, in Tropical Woods (New Haven) **24**: 35–38. Dec. 1930.

ber from *Castilla elastica* and *Ficus cotinifolia* (Moraceae), gums and resins from *Bursera Simaruba*, *Myroxylon Pereirae* and *Protium Copal*, starch from roots of *Zamia*, *Maranta* and *Manihot*, oil from seeds of *Attalea Cohune* (a palm) and *Jatropha Curcas*, soap from the berries of *Sapindus Saponaria*, and tannin from the bark of *Pithecolobium albicans* and *Rhizophora Mangle*.

Cosmetics are obtained from *Rhoeo discolor* (Commelinaceae) and *Calocarpum mammosum* (Sapotaceae), and perfume from *Acacia Farnesiana*.

Other miscellaneous plant products are the leaves of *Cordia dodecandra*, used for sandpaper, water vessels from the fruits of *Crescentia Cujete* (calabash tree), toys from the pods of *Pithecoctenium*, and whistles from the stems of *Jatropha Gaumeri*.

UNIVERSITY, ALABAMA

A list of algae from Missouri

FRANCIS DROUET

(WITH PLATES 18, 19)

The following list of species of algae is based on my collections in various parts of the state of Missouri during the past three years, and includes also any herbarium specimens of Missouri algae which have been called to my attention.

Several lists of algae have been reported from the state, all but one of which are from the Missouri Botanical Garden at St. Louis, by Hayden (1910), Spargo (1913), Moore and Karrer (1919), and Moore and Carter (1926). Few preserved specimens to support these identifications have been found. Many species appear in these lists which do not appear in my collections. Drouet (1930) reported 108 species from the vicinity of Columbia. These specimens have all been re-examined and are included in the present paper, which is intended to supplant, not to supplement, that of 1930.

The algal flora of Missouri is similar to that of the states bordering it. The state as a whole is not a definite geographical region; but, within its boundaries, three types of country can be distinguished.

The northern part of the state is glaciated and possesses a deep soil covering the underlying limestone. The streams are muddy for at least part of the year. Diatoms and species of *Cladophora* are the most abundant algae of these streams.

The southeastern part of the state is the low flood plain of the Mississippi and St. Francois Rivers. Drainage canals and shallow pools of standing water are characteristic. These bodies of water have been inadequately investigated. It appears, however, from my meager observations, that the algal vegetation is similar to that of ponds and shallow lakes throughout the state.

The Ozark or southern portion of the state is a rugged, hilly plateau with a maximum elevation of 1800 feet in Iron County. Clear, swift brooks flow over limestone and sandstone beds to the north, east, and south. These streams contain quantities of *Cladophora* spp., associated with diatoms and Zygnematables. In Gravois Creek, *Batrachospermum virgatum* forms an integral part of the submerged vegetation. This part of the state is peculiarly characterized by the presence of underground rivers which gush out of the earth as enormous springs. Big Spring, the largest of these, located in Carter County, discharged 223,000,000 gallons of water in one day, as measured by Rodhouse (1920) by means of a Price current meter. Rodhouse considers that the temperature of each of these large springs

remains at approximately 58°–60° F. during the entire year. The springs and their spring branches support in the spring and summer months a large subaquatic vegetation of *Rhizoclonium hieroglyphicum*, *Tribonema bombycinum*, *Lysigonium* sp., *Microspora Loefgrenii*, and *M. amoena*. Species of *Batrachospermum* occur in Bennett, Maramec, Gravois, Yancy Mills, and Round Springs. The subaërial algae are chiefly of species of *Vaucheria* and *Phormidium*. Representatives of the Oedogoniales, Desmidiaceae, Chlorococcales, and of the genus *Cladophora* are notably absent. In Maramec and Gravois Springs, a winter submerged association of vegetative *Vaucheria*, *Spirogyra*, and diatoms has been observed to replace the spring and summer vegetation.

A transitional region existing between the northern and Ozark areas includes the Missouri River valley and is characterized by the presence of clear or muddy streams and of numerous small springs. Some of these springs contain dissolved salts of iron and sulfur. At Chouteau Springs in Cooper County, hydrogen sulfide bubbles continuously through the water which issues from the springs. The retaining tiles are covered below the surface of the water with layers of *Oscillatoria chalybea*, *O. minima*, and sulfur bacteria. In the winter the tiles were found to be lined with *Calothrix parietina*, *Gloeocapsa* sp., and sulfur bacteria. The marsh through which the waters flow is covered with mats of *Enteromorpha intestinalis*. Small freshwater springs contain the usual submerged forms of *Stigeoclonium*, *Draparnaldia*, Zygnematales, *Tribonema*, and diatoms and the subaërial *Vaucheria* spp.

Artificial lakes, ponds, and smaller bodies of water contain the subaquatic species of *Pithophora*, Oedogoniales, Zygnematales, Chlorococcales, flagellates, and a variety of other groups. Desmids are usually few in both diversity of forms and number of individuals. Large bodies of water are rare in Missouri; the largest is the new Lake of the Ozarks in the valley of the Osage River. Our present knowledge of the algae of the submerged area furnishes a possibility of much interesting work on the origin and development of the vegetation of a large body of water.

Approximately 900 collections of algae have been preserved. The majority of these come from the central and southern parts of the state.

Collected material was examined in the living condition or in a 5 per cent aqueous solution of formalin. Each collection was then preserved in a small vial of 5 per cent aqueous formalin or of Pfeiffer's solution, as recommended by Hazen (1902). All of these vials are in my possession. Many specimens were dried and placed in the Herbarium of the University of Missouri. Specimens were identified according to the descriptions and keys in the large taxonomic works cited at the end of this paper; and,

as far as possible, these descriptions were compared with original diagnoses of species. Most of the specimens were compared with exsiccatae in the Phycotheca Boreali-americana and the American Algae. Dr. William Randolph Taylor, Dr. Gilbert Morgan Smith, and Dr. Tracy E. Hazen were so kind as to examine a few of the specimens. The exsiccatae from Missouri in the Herbarium of the Missouri Botanical Garden and plankton collections made by the U. S. Bureau of Fisheries from the Mississippi River bordering Missouri were also examined and are included in the list.

The Desmidiaceae and the flagellate groups have been identified, at least approximately, by the use of standard monographic keys and descriptions; but the lists of species of these groups are intended more to show the variety of such organisms within the state than to extend the knowledge or distribution of individual species.

I wish here to express my appreciation to Dr. H. W. Rickett and other members of the Department of Botany and to Dr. W. R. Taylor of the University of Michigan for guidance and kindly criticism during the progress of this work; to Dr. G. T. Moore and Dr. J. M. Greenman for the use of the library and herbarium at the Missouri Botanical Garden; to Miss Ada Hayden for the loan of her original sketches of Missouri algae; to Dr. M. M. Ellis for the use of the collections of the U. S. Bureau of Fisheries; and to the many interested people who were so kind as to collect specimens for me.

LIST OF SPECIES

The scheme of classification used here is based upon that of West and Fritsch (1927) and of Fritsch (1929), supplemented by that of the authors of Pascher's *Süsswasserflora*. Distribution of forms within the state is indicated by the names of counties following each citation. Names of collectors appear in italics.

CHLOROPHYCEAE

VOLVOCALES

CHLAMYDOMONAS COMMUNIS Snow. Boone.
CHLAMYDOMONAS GRACILIS Snow. Boone.
POLYTOMA UVELLA Ehr. Boone.
GONIUM PECTORALE Müll. Boone.
PANDORINA MORUM Bory. Boone (*Schmidt*), St. Clair.
EUDORINA ELEGANS Ehr. Boone, Lewis (*Ellis*).
EUDORINA ILLINOISENSIS (Kofoid) Pascher. Mississippi.
PLATYDORINA CAUDATA Kofoid. Camden.
SPHAERELLA LACUSTRIS (Gir.-Chantr.) Wittr. Mississippi.
VOLVOX sp. Boone (*Holtzwart*).

TETRASPORALES

GLOEOCYSTIS FENESTRALIS (Kütz.) A. Br. St. Louis (*Collins*).

TETRASPORA GELATINOSA (Vauch.) Desv. Jackson, Boone.

TETRASPORA LUBRICA (Roth) Ag. Boone, Lawrence (*Leake*).

TETRASPORA spp. Boone, Monroe.

CHLOROCOCCALES

CHLOROCOCCUM HUMICOLUM (Näg.) Rab. Boone.

CHARACIUM BRAUNII Bruegger var. Boone. (*Fig. 1.*)

> This form is somewhat smaller than the type but seems to correspond with the latter in the shape of the cell. Our plants measure $23-27\mu$ long and $3-7\mu$ wide.

CHARACIUM FALCATUM Schroeder. Boone.

CHLOROCHYTRIUM LEMNAE Cohn. Boone (*M. Johnson*).

PEDIASTRUM BORYANUM (Turp.) Men. Cooper.

PEDIASTRUM DUPLEX Meyen. Clay (*Elmore*), Lewis (*Ellis*), Mississippi.

PEDIASTRUM TETRAS (Ehr.)Ralfs. Boone, Mississippi.

HYDRODICTYON RETICULATUM (L.) Lag. Boone, St. Louis (*Pfeiffer, Hayden*).

CHLORELLA VULGARIS Beijerinck. Boone, Cooper, Maries.

ACANTHOSPHAERA ZACHARIASII Lemm. Boone.

OOCYSTIS LACUSTRIS Chodat. Cooper.

LAGERHEIMIA CITRIFORMIS (Snow) G. M. Smith. Mississippi.

TETRAEDRON LONGISPINUM (Perty) Hansg. Boone.

TETRAEDRON MINIMUM (A. Br.) Hansg. Boone.

TETRAEDRON MUTICUM (A. Br.) Hansg. Mississippi.

TETRAEDRON QUADRATUM (Reinsch) Hansg. Boone.

KERATOCOCCUS RHAPHIDIOIDES (Hansg.) Pascher. Boone.

ANKISTRODESMUS FALCATUS (Corda) Ralfs. Boone.

A. FALCATUS ACICULARIS (A. Br.) G. S. West. Boone.

A. FALCATUS SPIRILLIFORMIS G. S. West. Boone, Grundy (*Cunningham*), Hickory, Osage.

ANKISTRODESMUS LONGISSIMUS (Lemm.) Wille. Boone.

SELENASTRUM GRACILE Reinsch. Howard (*Petry*).

SELENASTRUM MINUTUM (Näg.) Collins. Mississippi, St. Clair.

DICTYOSPHAERIUM EHRENBERGIANUM Näg. Boone.

SCENEDESMUS ACUMINATUS MINOR G. M. Smith. Montgomery.

SCENEDESMUS ARMATUS (Chod.) G. M. Smith. Mississippi.

SCENEDESMUS BIJUGA (Turp.) Lag. Howell, Boone.

SCENEDESMUS CARINATUS (Lemm.) Chod. Hickory.

SCENEDESMUS DIMORPHUS (Turp.) Kütz. Caldwell (*Elmore*), Lewis (*Geisendorfer*), St. Clair, Montgomery.

SCENEDESMUS OBLIQUUS (Turp.) Kütz. Henry.

SCENEDESMUS OPOLIENSIS Richter. Clay (*Elmore*).

SCENEDESMUS QUADRICAUDA (Turp.) Breb. Boone, Lewis (*Geisendorfer*), Mississippi.

COELASTRUM MICROPORUM Näg. Boone, Cooper, Audrain, Mississippi, St. Clair, Vernon.

ULOTRICHALES

ULOTHRIX TENERRIMA Kütz. Boone, Lewis (*Geisendorfer*).

HORMIDIUM FLACCIDUM A. Br. *sens. ampl.* Boone, Pulaski.

STICHOCOCCUS SCOPULINUS Hazen. Boone (*Glen Huff*).

CYLINDROCAPSA GEMINELLA MINOR Hansg. Boone.

ENTEROMORPHA INTESTINALIS (L.) Grev. f. TENUIS Collins. Cooper. (*Figs. 2, 3.*)

> This form has been observed only in a marsh supplied with salt water containing dissolved hydrogen sulfide at Chouteau Springs in Cooper County. Collins (1909) points out that the plants may be the same as *E. intestinalis crispa* Ktz., but that Kützing has given an insufficient description for the variety. The type specimen of the forma *tenuis* is No. 125 of Tilden's American Algae, collected in 'artesian, running water' in South Dakota.

MICROSPORA AMOENA (Kütz.) Rab. Camden, Phelps, Morgan.

> This species and the next are found only in those collections from the large springs of the Ozarks.

MICROSPORA LOEFGRENII (Nordst.) Lag. Phelps, Pulaski.

MICROSPORA QUADRATA Hazen. Boone.

MICROSPORA STAGNORUM (Kütz.) Lag. Boone, Cooper, St. Louis (*Collins*).

MICROSPORA TUMIDULA Hazen. Boone, Hickory.

STIGEOCLONIUM LUBRICUM (Dillw.) Kütz. Dallas.

STIGEOCLONIUM TENUE (Ag.) Kütz. Boone, Jackson.

STIGEOCLONIUM spp. Jackson, Randolph, Monroe, Grundy (*Cunningham*).

DRAPARNALDIA ACUTA (Ag.) Kütz. Boone, Monroe, Hickory.

DRAPARNALDIA GLOMERATA (Vauch.) Ag. Boone.

DRAPARNALDIA PLUMOSA (Vauch.) Ag. Boone, Dallas, Cooper.

CHAETOPHORA ELEGANS (Roth) Ag. Boone, Reynolds, Lawrence (*Leake*).

CHAETOPHORA INCRASSATA (Huds.) Hazen. Boone, Miller, Morgan.

CHAETOPHORA PISIFORMIS (Roth) Ag. Boone.

MICROTHAMNION KUETZINGIANUM Näg. Boone.

MICROTHAMNION STRICTISSIMUM Rab. Clay (*Elmore*), Audrain, Callaway.

PROTODERMA VIRIDE Kütz. Dent, Marion (*Gulick*).

APHANOCHAETE REPENS A. Br. Boone, Grundy (*Cunningham*), Miller, St. Clair, St. Charles (*Ennis*), Ralls (*Gulick*).

PLEUROCOCCUS NAEGELII Chod. Boone, Jackson, Pemiscot (*Miller*), Cooper, Barry (*Leake*), Carroll (*Elmore*).

CLADOPHORALES

RHIZOCLONIUM HIEROGLYPHICUM (Ag.) Kütz. Boone, Camden, Shannon, Carter, Reynolds, Clay (*Elmore*), Pulaski, Benton, St. Clair, Johnson, Montgomery, Miller, Barry (*Leake*), Stone (*Leake*), Morgan, St. Louis (*Collins*).

CLADOPHORA CRISPATA (Roth) Kütz. ampl. Brand. Jackson, St. Francois (*Nahm*), Cole, Vernon, Caldwell (*Old*).

CLADOPHORA FRACTA (Dillw.) Kütz. ampl. Brand. St. Charles (*Ennis*), Ralls (*Gulick*), Montgomery.

CLADOPHORA GLOMERATA (L.) Kütz. ampl. Brand. Cooper, Boone, Camden, St. Clair (*H. F. Hand*), Jackson, St. Louis Co. (*Nelson, Holtzwari*), Miller, Clay (*Elmore*).

PITHOPHORA MOOREANA Collins. St. Louis (*Moore*).

PITHOPHORA OEDOGONIA (Mont.) Wittr. Boone, St. Louis (*Hayden*).

PITHOPHORA VARIA Wille. Clay (*Elmore*).

OEDOGONIALES

BULBOCHAETE sp. Boone.
OEDOGONIUM CAPILLIFORME (Kütz.) Wittr. St. Louis (*Pammel*).
OEDOGONIUM INTERMEDIUM Wittr. Dent, Howell.
OEDOGONIUM MARTINICENSE Hirn. Boone.
OEDOGONIUM PISANUM Wittr. Jackson.
OEDOGONIUM RUFESCENS Wittr. Audrain.
OEDOGONIUM spp. Common.

ZYGNEMATALES

ZYGNEMA INSIGNE (Hass.) Kütz. Boone.
ZYGNEMA STELLINUM (Müll.) Ag. Platte (*Holtzwart*), Jackson, Randolph (*Adams*).
ZYGNEMA (?) PECTINATUM (Vauch.) Ag. Moniteau.
SPIROGYRA AFFINIS (Hass.) Petit. Jackson (*J. & R. R. Drouet*).
SPIROGYRA BELLIS (Hass.) Cleve. Callaway.
SPIROGYRA COMMUNIS (Hass.) Kütz. Boone.
SPIROGYRA DECIMINA (Müll.) Kütz. Boone, Camden, Grundy (*Cunningham*).
SPIROGYRA ELLIPSOSPORA Transeau. Boone.
SPIROGYRA FLUVIATILIS Hilse. Boone, Miller.
SPIROGYRA GRACILIS (Hass.) Kütz. Jackson (*J. & R. R. Drouet*).
SPIROGYRA GREVILLEANA (Hass.) Kütz. Boone, Jackson (*J. & R. R. Drouet*).
SPIROGYRA IRREGULARIS Näg. Cedar.
SPIROGYRA JUERGENSII (Kütz.) Petit. Jackson.
SPIROGYRA LONGATA (Vauch.) Kütz. Reynolds.
SPIROGYRA PORTICALIS (Müll.) Cleve. Boone, Audrain.
SPIROGYRA SUBMAXIMA Transeau. Grundy (*Cunningham*).
SPIROGYRA VARIANS (Hass.) Kütz. Grundy (*Cunningham*).
SPIROGYRA WEBERI (Kütz.) Petit. Boone.
MOUGEOTIA VIRIDIS (Kütz.) Wittr. Mississippi.
PENIUM LIBELLULA (Focke) Nordst. Boone.
PENIUM MARGARITACEUM (Ehr.) Breb. Boone, Hickory.
CLOSTERIUM ACEROSUM (Schrank.) Ehr. Boone.
CLOSTERIUM LANCEOLATUM Kütz. Boone, Benton.
CLOSTERIUM LEIBLEINII Kütz. Callaway, Boone, Benton, Henry
CLOSTERIUM MONILIFERUM (Bory) Ehr. Boone, Camden, Jackson, Grundy (*Cunningham*), Pulaski, St Clair.
CLOSTERIUM PERACEROSUM G. S. West. Boone.
CLOSTERIUM PRITCHARDIANUM Arch. Boone.
CLOSTERIUM SUBTRUNCATUM W. & G. S. West. Boone, Morgan.
PLEUROTAENIUM MAXIMUM (Reinsch) Lund. Dent.
PLEUROTAENIUM TRUNCATUM (Breb.) Näg. Boone.
COSMARIUM UNDULATUM Corda. Dallas.
COSMARIUM spp. Common.
HYALOTHECA MUCOSA (Dillw.) Ehr. Randolph (*Adams*), Morgan, Ralls (*Gulick*).
DESMIDIUM SWARTZII Ag. Marion (*Gulick*).

SIPHONALES

VAUCHERIA AVERSA Hass. Randolph (*Adams*).
VAUCHERIA GEMINATA (Vauch.) DC. Boone, Jackson, Randolph (*Adams*), Miller, Marion (*Gulick*), Caldwell (*Old*).

VAUCHERIA ORTHOCARPA Reinsch. Cass (*J. & R. R. Drouet*), Grundy (*Cunningham*).
VAUCHERIA POLYSPERMA Hass. Boone, Callaway.
VAUCHERIA REPENS Hass. Dent, Benton, Johnson, Cole, St. Louis (*Collins*).
VAUCHERIA SESSILIS (Vauch.) DC. Shannon, Boone.
VAUCHERIA spp. Common.

HETEROKONTAE

BOTRYOCOCCUS BRAUNII Kütz. Boone, Vernon.
CHLOROBOTRYS REGULARIS (West) Bohlin. Boone.
TRIBONEMA BOMBYCINUM (Ag.) Derb. & Sol. Jackson, Howard, Phelps, Pulaski,
    Grundy (*Cunningham*), Morgan, Ralls (*Gulick*), Stone (*Leake*), Boone.
    f. TENUE Hazen. With *T. bombycinum*.
TRIBONEMA MINUS (Wille) Hazen. Boone, Dent, Morgan.
BOTRYDIUM GRANULATUM Grev. Boone, Howard (*Petry*).

CHRYSOPHYCEAE

DINOBRYON SOCIALE Ehr. Iron.

CRYPTOPHYCEAE

CHILOMONAS PARAMOECIUM Ehr. Boone.

DINOPHYCEAE

CERATIUM HIRUNDINELLA O. F. M. Boone.

EUGLENINEAE

EUGLENA ACUS Ehr. Howell.
EUGLENA DESES Ehr. Boone, Callaway.
EUGLENA ELONGATA Schew. Boone.
EUGLENA OXYURIS Schmarda. Boone.
EUGLENA PISCIFORMIS Klebs. Boone.
EUGLENA SANGUINEA Ehr. Boone, Reynolds, St. Louis?
EUGLENA SPIROGYRA Ehr. Boone, Benton.
EUGLENA SPIROIDES Lemm. Boone.
PHACUS PLEURONECTES (O. F. M.) Duj. Boone, Cooper, St. Clair, Morgan.
PHACUS LONGICAUDA (Ehr.) Duj. Boone, Howell.
TRACHELOMONAS ELEGANS Conrad. Lewis (*Geisendorfer*).
TRACHELOMONAS VOLVOCINA Ehr. Boone.
TRACHELOMONAS HISPIDA (Perty) Defl. Boone.

RHODOPHYCEAE

PORPHYRIDIUM CRUENTUM (Ag.) Näg. Boone, St. Louis (*Norton, Collins*).
BATRACHOSPERMUM BORYANUM Sirdt. *Identification by Wm. R. Taylor*. Phelps.
BATRACHOSPERMUM VIRGATUM (Kütz.) Sirdt. *Identification by Wm. R. Taylor*. Morgan.
BATRACHOSPERMUM spp. Dallas, Stone (*Leake*), Phelps, Shannon.

MYXOPHYCEAE

CHROOCOCCALES

MICROCYSTIS AERUGINOSA Kütz. Johnson.

APHANOCAPSA ELACHISTA W. & G. S. West. Cooper, Boone.

APHANOTHECE SAXICOLA Näg. St. Clair.

This form covers the rocks and ironwork about a spring in which hydrogen sulfide bubbles. It has been found in Missouri only at Monegaw Springs.

GLOEOCAPSA FUSCO-LUTEA (Näg.) Rab. Boone (*Petry*).

GLOEOTHECE LINEARIS Näg. St. Louis (*Collins*).

CHROOCOCCUS MINOR (Kütz.) Näg. Boone, Clay (*Elmore*), St. Clair.

CHROOCOCCUS MINUTUS (Kütz.) Näg. Boone, Morgan.

CHROOCOCCUS REFRACTUS Wood. Boone, St. Louis Co. (*Holtzwart*).

CHROOCOCCUS TURGIDUS (Kütz.) Näg. Boone, St. Louis Co. (*Holtzwart*), Benton, St. Francois (*Mosier*), Cooper.

CHROOCOCCUS TURICENSIS (Näg.) Hansg. Montgomery.

COELOSPHAERIUM NAEGELIANUM Ung. St. Charles (*Ennis*), Johnson. (*Fig. 4.*)

MERISMOPEDIA CONVOLUTA Breb. Cooper.

MERISMOPEDIA ELEGANS A. Br. Johnson.

MERISMOPEDIA GLAUCA (Ehr.) Näg. Dallas, Howell, Shannon, Boone, Texas, Benton, Johnson.

MERISMOPEDIA TENUISSIMA Lemm. Boone, Benton.

CHAMAESIPHONALES

CNCOBYRSA RIVULARIS (Kütz.) Geitler. Morgan.

CHAMAESIPHON INCRUSTANS Grun. Camden, Pulaski, Stone (*Leake*).

HORMOGONALES

SPIRULINA MAJOR Kütz. Franklin (*Holtzwart*), Henry, St. Clair, Randolph (*Adams*).

SPIRULINA NORDSTEDTII Gomont. Boone.

OSCILLATORIA AGARDHII Gomont. Reynolds, St. Louis (*Hus*).

OSCILLATORIA AMOENA (Kütz.) Gomont. Boone, St. Clair, Hickory, Cooper, Pettis.

OSCILLATORIA ANGUINA (Bory) Gomont. Boone, Miller, Lewis (*Geisendorfer*), Grundy (*Cunningham*).

OSCILLATORIA ANGUSTISSIMA W. & G. S. West. Boone, Jackson.

OSCILLATORIA BREVIS Kütz. Boone, Pulaski.

OSCILLATORIA CHALYBEA Mertens. Cooper.

OSCILLATORIA CURVICEPS Ag. Randolph (*Adams*). (*Fig. 5.*)

The trichomes of our material are 6.4–10μ wide, whereas those of the type are 10–17μ wide.

OSCILLATORIA FORMOSA Bory. Boone, Jackson, Howard, Randolph (*Adams*).

OSCILLATORIA LIMOSA Ag. Boone, Camden, Cooper Saline.

OSCILLATORIA MINIMA Giklhorn. Cooper. (*Fig. 6.*)

This alga grows, as Geitler (1925) points out, in water containing dissolved hydrogen sulfide. At Chouteau springs, the trichomes are associated with *O. chalybea* and sulfur bacteria. With dark field illumination, the trichomes reflect blue light. This phenomenon of *Blauglanz* Geitler says is characteristic of certain Oscillatorias of sulfur springs.

OSCILLATORIA ORNATA Kütz. Miller, Boone, St. Clair, Montgomery.

OSCILLATORIA PRINCEPS Vauch. Howell, Mississippi, Boone, Morgan, Benton, St. Louis (*Webber*), Dunklin (*Trelease*).

OSCILLATORIA PROBOSCIDEA Gomont. Camden, Shannon.

OSCILLATORIA SPLENDIDA Grev. Howell, Boone, Randolph (*Adams*), Miller, Morgan, St. Clair, Benton, Pettis, Cooper.

OSCILLATORIA SUBTILISSIMA Kütz. Boone, Morgan, Johnson.

OSCILLATORIA TENUIS Ag. Boone, Howell, 'Spring Park' (*F. W. D.*), Dunklin (*Trelease*).

O. TENUIS NATANS Kütz. Boone, Morgan.

O. TENUIS TERGESTINA (Kütz.) Rab. Howell, Shannon, Boone, Randolph (*Adams*).

PHORMIDIUM AUTUMNALE (Ag.) Gomont. Boone, Camden, Monroe, Clay (*Elmore*), Pulaski, Morgan, Stone (*Leake*).

PHORMIDIUM FOVEOLARUM (Mont.) Gomont. Scott, Lewis (*Geisendorfer*).

PHORMIDIUM FRAGILE (Men.) Gomont. Boone.

PHORMIDIUM UNCINATUM (Ag.) Gomont. Phelps, Clay (*Elmore*), Randolph (*Adams*).
   The small species of *Phormidium* and *Lyngbya* are often difficult to distinguish. The amount of confluence and diffluence of the sheaths is an uncertain criterion, especially since the volume and consistency of the sheath surely depend upon the internal condition of the protoplasm and upon the character of the environment. In this environment, bacteria which destroy the jelly are always present and are usually abundant. In Missouri, at least, the two genera are in need of critical examination, especially the smaller species.

LYNGBYA MARTENSIANA Men. Boone, St. Louis Co.(*Holtzwart*),Morgan, Cooper, Bates.

LYNGBYA OCHRACEA (Kütz.) Thuret. Boone.

LYNGBYA spp. Franklin (*Holtzwart*), Henry.

SYMPLOCA MUSCORUM (Ag.) Gomont. Boone, Johnson.

SCHIZOTHRIX sp. St. Clair.

HYDROCOLEUS RAVENELII Wolle. Boone.

MICROCOLEUS LACUSTRIS (Rab.) Farlow. Cooper, Henry, Montgomery.

MICROCOLEUS PALUDOSUS (Kütz.) Gomont. Boone.

MICROCOLEUS SOCIATUS W. & G. S. West. Cole, Moniteau. (*Fig. 7.*)

MICROCOLEUS VAGINATUS (Vauch.) Gomont. Boone, Miller, Henry, St. Clair, St. Charles (*Ennis*), Ralls (*Gulick*), Moniteau.

APHANIZOMENON FLOS-AQUAE (L.) Ralfs. Johnson, St. Louis Co. (*Holtzwart*).
   Our material is all of the minimum dimensions described for the type and almost coincides with those of the Russian *A. Flos-aquae Klebahnii* Elenkin.

NOSTOC COMMUNE Vauch. Boone.
   Although this alga has been collected from the same locality at least once a month for two years and has been repeatedly grown in the laboratory, no gonidia have been observed on it.

NOSTOC MUSCORUM Ag. Boone, Osage.

NOSTOC VERRUCOSUM (L.) Vauch. Phelps, Dent.

ANABAENA CATENULA (Kütz.) Born. & Flah. St. Louis (*Hunt*).

ANABAENA HALLENSIS (Jancz.) Born. & Flah. Boone.

ANABAENA INAEQUALIS (Kütz.) Born. & Flah. Grundy (*Cunningham*), Jackson, Boone, Callaway. (*Fig. 8.*)
   Tilden (1910) has noted in her diagnosis of this species that the gonidia are

remote from the heterocysts; but her figures show them also contiguous to the heterocysts, as in our specimens.

ANABAENA TORULOSA (Carm.) Lag. Mississippi.

(?) ANABAENA sp. Shannon. (*Fig. 9.*)

The trichomes of this material are devoid of heterocysts and gonidia, but the shapes of the cells and the habit of the plants make it plausible to call the form an *Anabaena*. Whether or not the material represents a new species of *Pseudanabaena* must be learned by future collecting.

CYLINDROSPERMUM MAJUS Kütz. Boone, Jackson.

PLECTONEMA WOLLEI Farlow. St. Louis Co. (*Holtzwart*).

SCYTONEMA MIRABILE (Dillw.) Born. Montgomery.

SCYTONEMA OCELLATUM Lyngb. Boone, St. Louis (*Collins*).

TOLYPOTHRIX TENUIS Kütz. Randolph (*Adams*).

HOMOEOTHRIX ENDOPHYTICA Lemm. Morgan. (*Fig. 10.*)

I have found no previous record of *Homoeothrix* in America; but the conspicuous absence of heterocysts and the striking agreement of the habit and form of the filaments with the description by Geitler (1925) force me to call this alga *H. endophytica*. It differs from *Calothrix fusca* (Kütz.) Born. & Flah. in the width of the sheaths and in the absence of heterocysts. The specimens have cells 6–9μ wide and 1.5–2μ long at the middle and base of the trichome, and they are imbedded in the thalli of *Batrachospermum virgatum* from the spring branch at Gravois Mills, Morgan Co.

CALOTHRIX BRAUNII Born. & Flah. Cooper.

CALOTHRIX CASTELLII (Massal.) Born. & Flah. Hickory.

CALOTHRIX PARIETINA (Näg.) Thuret. Boone, Cooper.

RIVULARIA sp. Boone.

DEPARTMENT OF BOTANY
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Explanation of plates

PLATE 18

Photographs by Dr. H. W. Rickett.

Fig. 1. Big Spring in Carter County, near Van Buren. This is the largest spring in Missouri. Notice the enormous volume of water which issues from such a spring.

Fig. 2. The lower spring branch of Maramec Spring, six miles southeast of St. James in Phelps County. This spring, according to Rodhouse (1920), discharged 88,000,000 gallons of water in one day. Notice the excellent algal habitats along the edge of the brook. The conspicuous vegetation consists mostly of *Radicula Nasturtium-aquaticum*.

PLATE 19

These figures were made with the aid of a Bausch and Lomb camera lucida and a Bausch and Lomb binocular microscope with various combinations of the 6×, 10×, and 25× oculars and the 16 mm., 4 mm., and 1.9 mm. objectives.

Fig. 1. *Characium Braunii* var. ×1000.

Fig. 2. *Enteromorpha intestinalis* f. *tenuis*. Cross section of the cells of the frond. The inner membrane is on the left hand side. ×400.

Fig. 3. *Enteromorpha intestinalis* f. *tenuis*. Surface view of the cells. ×400.

Fig. 4. *Coelosphaerium Naegelianum*. a. Typical colony. ×150. b. Cells showing pseudovacuoles. ×600.

Fig. 5. *Oscillatoria curviceps*. ×400.

Fig. 6. *Oscillatoria minima*. ×1000.

Fig. 7. *Microcoleus sociatus*. Ends of two trichomes. ×1000.

Fig. 8. *Anabaena inaequalis*, showing gonidia contiguous to a heterocyst. ×1000.

Fig. 9. (?) *Anabaena* sp. ×1000.

Fig. 10. *Homeothrix endophytica*. a. A filament and a trichome. ×350. b. Detail of cells of a trichome. ×1500.
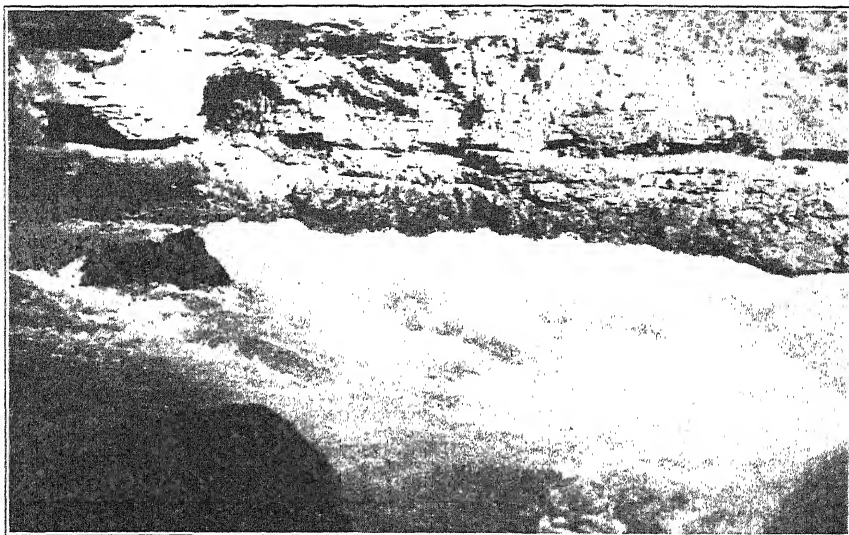
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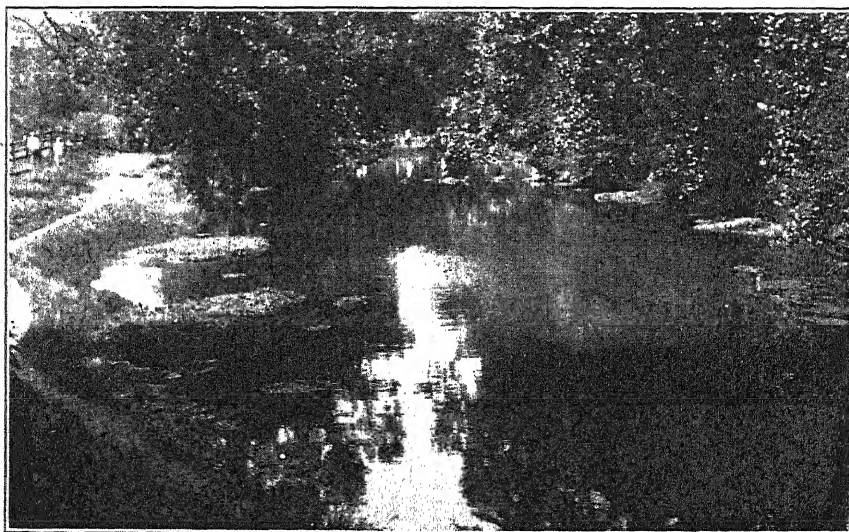
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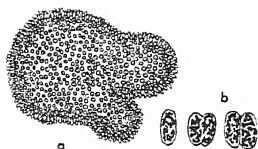
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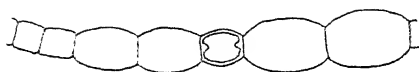
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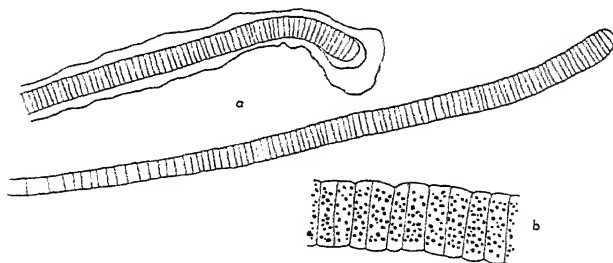
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DROUET: ALGAE FROM MISSOURI

INDEX TO AMERICAN BOTANICAL LITERATURE

1928–1932

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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Tertiary pollen

I. Pollen of the living representatives of the Green River flora

R. P. WODEHOUSE

(WITH PLATES 20–22 AND THREE TEXT FIGURES)

It is the common complaint among paleobotanists that is is impossible to identify the pollen found in Tertiary deposits because there are no adequate descriptions and keys to the living species. In order to overcome completely this disability it would be necessary to acquire a familiarity with the pollen-grain forms of nearly every living species of flowering plant, a task far too great to be encompassed within the span of a single life. The next best thing is to acquire a familiarity with the living representatives of the known fossil flora of the formations in question, and to supplement this with a knowledge of the pollen-grain forms of as many as possible of the wind pollinated species which might have contributed their pollen to the deposits and yet not have grown near enough to the places of deposition to be otherwise represented. These latter I shall treat at considerable length in my book[1] which is now in press. The present paper presents my studies on the pollen of the remaining living representatives of the Green River flora of which material was available, and it is hoped that it will further assist in the identification of at least some of the many species found in the Green River shales. I plan to make the pollen of the Green River formation the subject of the second paper of this series treating Tertiary pollen.

The enormous numbers of beautifully preserved pollen grains in the Green River shales have frequently been commented upon by investigators of that formation. As long ago as 1917, C. A. Davis recorded, in Winchester's paper on The Oil Shales of the U. S. A., the presence of *Picea* and *Pinus* pollen. Bradley (1929), in his discussion of the fresh water algae of the Green River formation of Colorado says: "Organic matter consists of complete or fragmentary organisms such as algae, fungi, protozoa, insects and parts of higher plants, as spores pollen grains or minute pieces of tissue," and again (1931): "Pollens in great numbers and diversity occur in the oil shale, and many of them show their structural characters with fair clarity. If these pollens could surely be referred to their proper genera they would shed much additional light upon the flora of the Green River epoch. Unfortunately the morphology of pollen grains is imperfectly known, and consequently they have never been accurately correlated with classified plants."

[1] Morphology of the pollen grains, Charles C Thomas, publisher.

Unquestionably a greater knowledge of these pollen grains would correspondingly extend the known flora of the formation. For example Brown (1929) states: "The presence of conifers in this flora, hitherto indicated only by pollen grains in the oil shale, is now further established by the finding of what appears to be coniferous leaves and a winged seed." It so happens that pollen grains of the winged-grained Abietineae, such as *Picea* and *Pinus* are among the commonest in the shales, yet, as may be gathered from the above statement, the occurrence of other parts of the trees is relatively infrequent. This is probably because the Abietineae of that epoch were mostly upland species, not favorably situated for their preservation in the low-lying lakes and ponds in which the materials of the shales are believed to have been deposited; but the pollen, being buoyant and carried great distances by air currents, could well come to rest in such places even though the trees grew many miles distant. It is to be expected, therefore, that in the shales will be found the pollen of many species which had scarcely any chance of being otherwise preserved. Furthermore, many of the identified plant fragments of the Green River flora are of species which, judged by their modern representatives, must have shed in that epoch a great abundance of pollen well adapted to preservation. Finding the pollen of such species in the shales would serve as a valuable check on identification based on fossil leaves or other fragments. Conversely the absence of the pollen of these species might cast some doubt upon the correctness of identification based upon small or indefinite fragments of the plants.

The beauty and perfection of the preservation of such minute and delicate structures as pollen grains is a constant source of admiration and wonder. Some of the grains are as perfectly preserved in the material of the shales as if they had been imbedded in celloidin or balsam expressly for microscopic examination. Obviously the principal thing that is needed to render this beautiful record available is a more complete knowledge of the living representatives of that flora.

"The Green River is a Middle Eocene formation, about 2000 feet in thickness and of threefold character, comprising a lower group of light brown to buff sandy calcareous shale, and a middle group of darker shale, and an upper group of light colored sandy shale. The formation originally covered an area about 300 by 150 miles in the contiguous corners of Colorado, Utah and Wyoming, but erosion subsequent to the time when this area ceased to be a basin of lacustrine deposition and was elevated several thousand feet, has deeply dissected parts of it and has thereby isolated patches of the formation." (Brown, 1929.) One of these areas, the Piceance Creek basin, where the Green River formation is now exposed,

is about 95 miles long from north to south, and about 46 miles wide. Another, the Uinta Basin, where the formation is exposed, is a strip about 135 miles long from east to west and 46 miles wide at the widest place. There are two other areas of comparable extent, lying to the north of the Uinta Mountains in Wyoming, but these have been less fully studied. The location and distribution of these areas are shown in the maps of Bradley's paper (1931).

The flora of this ancient formation, as far as it is at present known, includes about 130 species. These are predominantly subtropical mesophytes, totally unlike the flora now occupying the region. According to Brown (1929) the presence of such forms as palms, *Planera* and *Acrosticum* which require an abundance of rain fall and a warm climate, together with such species as *Quercus, Populus, Betula* and *Liquidambar* "point to the conclusion that this flora grew in a warm temperate region, a part of which, at least, received a plentiful supply of rain." Such a climate is probably not duplicated in the world today but "the climatic conditions of the southeastern Gulf states plus that of parts of the Great Valley of California would . . . roughly approximate the Green River Lake Area." As will be seen from looking over the following lists, the species which are represented in the Green River flora belong predominantly to groups having their centers of concentration now in Mexico, Central America and the northern part of South America, as if the climatic changes which have taken place since the Green River epoch have been such as to force the ancient flora southward even as far as equatorial America. Whether this was the case, or the Green River flora was but a northward extension in Eocene times of a southern flora is still an open question.

The Green River Flora

A list of the families and genera compiled from Knowlton (1923) and Brown (1929)

CONIFERALES: *Taxites, Picea.*

SPARGANIACEAE: *Sparganium.*

GRAMINEAE: *Arundo.*

CYPERACEAE: *Cyperus, Cyperacites.*

ARECACEAE: *Geonomites, Sabal, Flabellaria.*

PONTEDERIACEAE: *Pontederia.*

JUNCACEAE: *Juncus.*

NYMPHAEACEAE (Cabombaceae): *Brasenia.*

SALICACEAE: *Salix, Populus.*

MYRICACEAE: *Myrica, Comptonia.*

JUGLANDACEAE: *Hicoria, Juglans.*

BETULACEAE: *Betula.*

FAGACEAE: *Quercus.*

ULMACEAE: *Planera, Celtis.*

MORACEAE: *Ficus.*
PROTEACEAE: *Lomatia, Banksia.*
LAURACEAE: *Oreodaphne, Pinelea.*
ROSACEAE: *Chrysobalanus, Amygdalus.*
CRASSULACEAE: *Sedum.*
LEGUMINOSAE: *Cassia, Dalbergia, Leguminosites, Sophora.*
MIMOSACEAE: *Mimosites.*
MALPIGHIACEAE: *Banisteria.*
SIMARUBACEAE: *Ailanthus.*
ANACARDIACEAE: *Rhus, Schmaltzia, Anacardites.*
CELASTRACEAE: *Celastrophyllum, Euonymus, Maytenus.*
SAPINDACEAE: *Thouinia, Sapindus.*
ACERACEAE: *Acer.*
AQUIFOLIACEAE: *Ilex.*
TILIACEAE: *Grewiopsis.*
RHAMNACEAE: *Zizyphus.*
VITACEAE: *Cissus. Parthenocissus.*
STERCULIACEAE: *Sterculia.*
TERNSTROEMIACEAE: *Ternstroemites.*
OLEACEAE: *Fraxinus.*
APOCYNACEAE: *Apocynophyllum, Apocynospermum.*
MYRTACEAE: *Eucalyptus.*
ARALIACEAE (Aricaceae): *Aralia.*
ERICACEAE: *Andromeda.*
CAPRIFOLIACEAE: *Sambucus.*
CUCURBITACEAE: *Cucurbita.* ·
COMPOSITAE: *Achaenites cichorioides.*

KEY TO THE POLLEN GRAINS OF THE FAMILIES OF THE LIVING REPRESENTATIVES OF THE GREEN RIVER FLORA[2]

A. Germinal apparatus consisting of a single pore or furrow, or rarely of two parallel furrows (MONOCOLPATE).

  I. Germinal apparatus consisting of a single furrow, more or less well defined, elongate.

    1. Provided with two lateral bladders.....................Abietineae (M).[2]

    2. Not provided with lateral bladders.

      a. Furrow always long and narrow, not provided with an operculum.

        i. Grains 19–30μ long................................Arecaceae (M).

        ii. Grains over 50μ long..................Cabombaceae (Nymphaeaceae).

      b. Furrow usually broad and always provided with an operculum..........
                              Nymphaeaceae (proper).

  II. Germinal apparatus a single more or less rounded or irregular-shaped pore.

    1. Pore small and round, slightly elevated and provided with an operculum; exine smooth..Gramineae (M).

    2. Pore not elevated and not provided with an operculum.

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[2] The pollen of some of the families and genera mentioned in the following key is not described further in the present work. These will be described and illustrated in the "Morphology of Pollen Grains," indicated by 'M.'

a. Exine reticulate, extremely thin; pore clearly defined........Sparganiaceae.
b. Exine not reticulate, extremely thin; pore not clearly defined.
    i. Grains in tetrahedral tetrads. Pore represented by a thin and elastic area
      of the exine.....................................Juncaceae (M).
    ii. Grains not in tetrads. Pore represented by an irregular granular area or
      a group of small rifts in the thin exine...............Cyperaceae (M).
III. Germinal apparatus consisting of two elongate parallel furrows............
                                       Pontederiaceae.
B. Germinal furrows or pores entirely absent, or represented only by scarcely visible
  and nonfunctional vestiges (ACOLPATE).
  I. Intine thick, expanding when moist. Exine thin and transparent, grains spheroidal.
    1. Exine flecked with granules of darkly staining material. Grains 25–30μ in
       diameter.....................................Taxaceae (Taxus) (M).
    2. Exine conspicuously warty. Grains 75–105μ in diameter.........Musaceae.
                                             Cannaceae.
    3. Exine covered with small sharp spines. Grains 25–65μ in diameter..Lauraceae.
  II. Intine not excessively thick; exine not spiny or warty.
    1. Grains single and ovoid, triangular or irregular in shape. Exine smooth or scurfy
                                           Cyperaceae (M).
    2. Grains united in tetrads................................Juncaceae (M).
    3. Grains united in flattened groups of 16, occasionally 8 or 32. Furrows vestigial,
       represented by slight linear depressions in the exine on the outer surfaces of
       the grain.....................................Mimosaceae (M).
C. Germinal apparatus consisting of three or more furrows or pores, or both, in which
  case the pores are enclosed by the furrows.
  I. Furrows present, with or without pores, generally three but when more than three
    arranged in the trischistoclasic system (FURROWED GRAINS).
    1. Furrows fully functional, generally three. Occasionally some of the grains may
       have more furrows arranged in the trischistoclasic system (TRICOLPATE).
      a. Exine provided with well developed spines or vestiges of them, not bristly.
        i. Exine without a lacunar pattern.
          x. Spines short, conical and sharp pointed.............Astereae (M).
          y. Spines greatly reduced or vestigial.................Ambrosieae (M).
        ii. Exine with a well developed lacunar pattern (Echinolophate)..........
                                       Cichorieae (M).
      b. Exine without spines or vestiges of them.
        i. Exine reticulate or deeply pitted.
          x. Reticulations coarse.
             aa. Furrow membranes smooth. Grains more then 19μ in diameter.
               AA. Reticulations isodiametric........................Vitaceae.
               BB. Reticulations elongate........................Simarubaceae.
            bb. Furrow membranes granular.
               AA. Grains more than 20μ in diameter.
                 xx. Grains ellipsoidal or spheroidal................Sterculiaceae.
                 yy. Grains flattened, triangular....................Araliaceae.
                 zz. Grains oblate spheroidal; some with four furrows...........
                                 Oleaceae (Fraxinus) (M).
            BB. Grains less than 20μ in diameter..............Salicaceae (M).

y. Reticulations very fine, or exine merely pitted.
   aa. With or without transverse furrow; exine pitted....Anacardiaceae.
   bb. Without transverse furrows; exine reticulate.
      AA. Pore sharply defined. Grains 17–26μ in diameter..Caprifoliaceae.
      BB. Pore not sharply defined.
         xx. Grains 16–35μ in diameter..................Celastraceae.
         yy. Grains 35–45μ in diameter.......Cucurbitaceae (Ibervillea).
ii. Exine thick, coarsely pebbled in appearance, shading off to the finer texture of the stiff furrow membrane.............Aquifoliaceae (Ilex) (M).
iii. Exine faintly granular or quite smooth.
   x. Grains more than 24μ in diameter.
      aa. Without internal hyaline wedges...................Aceraceae.
                               Leguminosae.
      bb. With three internal hyaline wedges, directed from the center of the grain towards the germ pores....................Fagaceae (M).
y. Grains less than 24μ in diameter, not provided with internal hyaline wedges.
      aa. Grains decidedly oblately flattened, 17–18μ in diameter, with extremely large and clearly defined germ pores.......Crassulaceae.
      bb. Grains spheroidal, ellipsoidal or only slightly flattened.
         AA. Pores large and clearly defined.
            xx. Transverse furrow present...................Castanea (M).
            yy. Transverse furrow absent................Ternstroemiaceae.
         BB. Pores not clearly defined, represented only by a swelling of the furrow membrane...........................Sapindaceae.
  iv. Exine covered with closely packed fine bristles. Grains about 85μ in diameter....................................Cucurbitaceae (Luffa).
2. Furrow reduced, scarcely or not at all functional in accommodating changes in volume, generally three.
  a. Grains united in tetrahedral tetrads, with the furrows of adjacent grains contiguous and continuous across the sutures with those of their neighbors....
                                   Ericaceae.[3]
  b. Grains not in tetrads.
   i. Furrows more or less deeply sunken pits, each almost coinciding in extent with its enclosed germ pore.
      x. Exine provided with spines or vestiges of them...................
                      Ambrosieae (Ambrosia etc.) (M)
      y. Exine not provided with spines.
         aa. Grains about 35μ in diameter..............Tiliaceae (Tilia) (M).
         bb. Grains about 20–25μ in diameter...................Myrtaceae.
   ii. Furrows inconspicuous shallow streaks..................Rhamnaceae.
3. Furrows nonfunctional in accommodating changes in volume, not tapering, with broad rounded ends; always more than three, arranged in the trischistoclasic system...Malpighiaceae.
II. Furrows, in the ordinary sense, absent, but pores present (PORED GRAINS).
  1. Pores generally more than two.
   a. Pores surrounded by a subexineous thickening (aspidate).

[3] Bowers (1931).

     i. Pores protruding conspicuously, giving the grain an angular appearance.
       x. Grains 11–23μ in diameter..........................Moraceae.
       y. Grains 20–30μ in diameter..........................Betulaceae.
                                            Myricaceae.
    ii. Pores not protruding conspicuously.
       x. Pores more or less crowded into one hemisphere.........Juglandaceae.
       y. Pores not crowded into one hemisphere; generally three equally spaced
          around the equator, or a larger number irregular-distributed..........
                                      Ulmaceae (Celtis).
  b. Pores not surrounded by a subexineous thickening.
    i. Pores more than 7 (generally 9–13), with opercula, not arranged around
      the equator. Grains spiny, 130–200μ in diameter.....................
                          Cucurbitaceae (Cucurbita, Lagenaria).
    ii. Pores 4–7 (occasionally 3), arranged around the equator, without opercula.
       x. Grains oblate spheroidal, 25–35μ in diameter; pores elliptical.........
                           Ulmaceae (Ulmus and Planera).
       y. Grains not oblately flattened, about 27μ in diameter; pores circular, sur-
         face warty........Malpighiaceae (Heteropterys Gayana, Malpighia).
    iii. Pores always three; grains flattened, and triangular or star shaped, about
      33μ in diamefer..............................Proteaceae (Lomatia).
  2. Pores always only two; grains crescent shaped........Proteaceae (Banksia).

SPARGANIACEAE

The family comprises only the following genus. It is regarded as closely related to Typhaceae. This view is abundantly sustained by the similarity of their pollen-grain forms which amounts almost to identity except that, as far as I know, the grains of species of *Sparganium* never occur in tetrads, while those of at least one species of *Typha* (viz. *T. latifolia*) always occur in tetrads.

SPARGANIUM L. Grains spheroidal or somewhat irregular in shape, 22.8–23.9μ in diameter, with a single germ pore, approximately circular in outline, 2.8–5.7μ in diameter, its membrane bearing a few darkly staining flecks. Exine coarsely reticulate, rather thin, and collapsing irregularly without reference to the position of the germ pore, in spite of the stiffening effect of the reticulate thickening of the exine. Intine thick throughout and always a little thicker in the region immediately underlying the germ pore. These grains are virtually indistinguishable from those of *Typha angustifolia* L. which have been described elsewhere (M.[2]).

The genus comprises about 22 species of low marsh or pond herbs which are all rather closely related; widely distributed in temperate and cold regions. They are monoecious, and shed large amounts of light, airborne pollen, but less than that of *Typha*, to which they bear many resemblances.

SPARGANIUM ANDROCLADUM (Engelm.) Morong. (fig. 13). Grains as in the generic description.

Newfoundland to Minn., Fla. and La. June–Aug.

SPARGANIUM ACAULE (Beeby) Rydb. Grains as in the generic description, but may be distinguished from those of the preceding species by their slightly coarser reticulum.

In swamps and on muddy shores. Newfoundland to Iowa, S. Dak. and Va. July–Sept.

PONTEDERIACEAE

PONTEDERIA CORDATA L. (Fig. 17). Grains somewhat ellipsoidal in outline, about $45.5 \times 48\mu$. Exine thick and rigid with a slightly granular texture. Furrows two, long, reaching almost from end to end of the grain. When the grain is expanded they are broad and of uniform width throughout their length, abruptly rounded at their ends; their membranes are smooth and sharply distinguished from the thick granular exine. The furrows are not diametrically opposite each other, but are displaced to one side of the grain, giving it a distinctly bilateral form in which a ventral and dorsal surface may be distinguished. The dorsal surface occupies nearly two thirds of the whole, arches throughout its length and projects laterally, overhanging the furrows and projecting beyond the margins of the ventral side, which is of smaller extent and less arched (fig. 8). The dorsal and ventral surfaces are separated from each other throughout most of their length by the two furrows but are joined to each other by a narrow isthmus at each end. The texture and thickness of the exine of dorsal and ventral surface is alike.

The presence of two furrows is certainly an anomalous condition among the grains of the Monocotyledons, since those of this group are predominantly monocolpate, unless acolpate by reduction. An explanation of this anomaly is offered by an analogous condition found among the grains of some of the Nymphaeaceae which are likewise characteristically monocolpate. In the grains of *Castalia* the furrow occupies the greater part of the ventral surface, but is almost entirely covered over by an extraordinarily large operculum. In most of the grains of this species this is not connected at any point to the exine of the general surface, being suspended and surrounded by a delicate furrow membrane. In a few grains, however, particularly those that are elongate in form, the operculum is connected with the exine of the general surface by a narrow isthmus at each end, thus dividing the encircling furrow membrane into two halves and giving them the appearance of two separate furrows. By analogy it therefore appears that in the grains of *Pontederia* the smaller ventral side is morphologically the operculum, and the two furrows represent the two halves of its encircling membrane. This interpretation is further substantiated by

the fact that in some grains of this species the isthmuses connecting the dorsal and ventral surfaces are extremely narrow and occasionally one of them even absent.

The Pickerel Weeds are semiaquatic herbs growing about the borders of ponds and streams, Nova Scotia to Minnesota, south to Florida and Texas. June–Oct. The genus includes about 8 species, native of America; while the family Pontederiaceae comprises about 5 genera and 25 species, inhabiting fresh water in the warm and temperate regions of America, Africa and Asia.

HETERANTHERA DUBIA (Jacq.) MacM. (*Schollera graminea* Gray). Grains similar to those of *Pontederia*, ellipsoidal, about 61μ long. Exine coarsely rough. The two furrows are similar to those of *Pontederia* in their curious one-sided arrangement and probably admit of the same interpretation, but differ from the latter in being covered completely over by exine of the same appearance as that of the general surface of the grain—they are merely longitudinal depressions.

Small aquatic plants with aerial flowers. Que. to Ore., south to Fla. and Mexico. July–Oct.

MUSACEAE

HELICONIA BIHAI L. (fig. 14 type). Grains entirely without furrows or pores, when fully expanded spherical, about 75–85μ in diameter. Exine exceedingly thin and transparent, but covered with numerous small opaque wart-like projections. Intine exceedingly thick and transparent, but in optical section exhibiting a radially striate appearance. This form of grain bears a remarkably close resemblance to that of the Lauraceae (q. v.).

A striking plant resembling the cultivated banana. West Indies, Central and South America. The genus includes 30 or 40 species in the American tropics, sometimes planted for their large banana-like foliage.

MUSA PARADISIACA var. SAPIENTUM Ktze. (*M. sapientum* L.). Grains similar to those of the type, except that the intine is less thick and swells less when moistened; 94–102μ in diameter; a large proportion of the grains are abortive and empty.

A tall plant, 10–30 ft. high with drooping spikes of fruit, native of India but widely cultivated in tropical countries. The genus includes 50 or more species native in the tropics of the Eastern Hemisphere.

CANNACEAE

CANNA GENERALIS Bailey. Grains similar to those of the *Heliconia* type, but with the wart-like protuberances of the exine more prominent and almost spine-like, about 1μ high and about 11μ apart. Grains 75–90μ in diameter, with the intine 15–22μ thick.

The common garden Canna, exists in many varieties which are the result of hybridization and breeding. The genus contains about 50 species of wide distribution in the Western Hemisphere. It is the only genus of the family Cannaceae, and is regarded as being closely related to the Musaceae.

CABOMBACEAE (Nymphaeaceae in part)

Grains long-ellipsoidal, monocolpate, 57–87μ long, and when fully expanded, about two thirds as broad. The furrow reaches almost the entire length of the grain; when expanded it is rather broad, with rounded ends and not tapering, often contorted and asymmetrically placed. Its membrane is either granular and broken by irregular rifts, or apparently lacking. When dry the furrow is tucked deeply in and appears as a narrow groove. In this condition the grain is only about one half of its expanded width, but is of the same length. Exine rather thick and stiff, often splitting longitudinally on the dorsal side, its surface granular or marked by conspicuous striae.

Aquatic perennial herbs, with both submerged and floating leaves and aerial flowers. Two genera and about five species of wide distribution in fresh-water lakes and streams. These two genera are frequently regarded as belonging to the Nymphaeaceae, and indeed are treated as such by Knowlton. But the form of their pollen grain bears no resemblance to those of the Nymphaeaceae, beyond being monocolpate, and therefore suggests that no relation really exists between the families. Or possibly they are both derived as separate stocks from the Bennettitales.

BRASENIA SCHREBERI Gmel. (*B. peltata* Pursh). fig. 19. Grains ellipsoidal, about 46×57μ; the single furrow generally asymmetrically placed and more or less contorted, without a well developed furrow membrane, appearing as an expanded rift through the exine. Exine finely granular, occasionally the granules tending to be linearly arranged, fragmented along the margins of the furrow. Intine thick throughout and thicker in the region underlying the furrow.

An aquatic herb with floating leaves and aerial flowers; in slow streams and ponds. Nova Scotia to Fla., Man., Neb. and Tex. also in Cuba and Mexico, and on the Pacific coast.

CABOMBA AQUATICA Aubl. Grains similar in general form to the *Brasenia* type; somewhat various in size, as if a large proportion of them were defective. Normal grains, when fully expanded, about 49×73μ; furrow broad, straight or contorted, with its membrane composed of coarse granules. Exine rather firm, markedly striate with longitudinal granular striae. When dry the furrow is tucked in tightly and deeply, causing the grain to assume an extremely elongate form. Mexico.

CABOMBA CAROLINIANA Gray. Grains indistinguishable from those of *C. aquatica*.

In ponds and slow streams. Mo. to Ill. to N. C. and south to Fla. and Tex. May–Aug.

MYRICACEAE

COMPTONIA PEREGRINA Coult. (*Myrica asplenifolia* L.) figs. 11, 16. Grains similar to those of birch, about 27μ in diameter, generally with three pores equally spaced around the equator, but extremely variable in this respect; frequently with two to five pores irregularly arranged, often all crowded into one hemisphere. Germ pores aspidate with their apertures circular or somewhat elliptical, 3.5μ in diameter. Texture nearly or quite smooth, or faintly granular around the pores.

A monoecious aromatic shrub. Nova Scotia to Man., Mich., Ind., Tenn. and N. C. Flowers in spring shedding large amounts of air-borne pollen. The family comprises about 35 species of shrubs or small trees of wide distribution in warm and temperate regions almost throughout the world.

MYRICA GALE L. Grains essentially as in *Comptonia peregrina.*

A small dioecious shrub along streams and ponds Newfoundland to Alaska, southern N. Y., Va., Mich. and Wash. Also Europe and Asia. Wind pollinated. April and May.

LAURACEAE

The grains of this family, as far as these observations have gone, are characterized by their lack of pores or furrows, the enormous thickening of their intine and the thinness of their exine which bears numerous characteristic spines. In size they range from about 25–65μ in diameter.

The family comprises about 1000 species, in about 40 genera, of trees and shrubs of wide distribution, principally in the tropics.

1. Grains 25–35μ in diameter, spines 2–3μ apart.
   i. Grains 25–30μ in diameter; intine about 3μ thick, and spines about 2.3μ apart....
      Ocotea flavescens.
   ii. Grains 31–35μ in diameter, intine about 4μ thick, spines about 2.4μ apart......
      Benzoin aestivale.
2. Grains 48–64μ in diameter; spines 4.6μ apart.
   i. Intine about 9μ thick, spines about 5.7μ apart................*Laurus nobilis.*
   ii. Intine about 15μ thick, spines about 4.6μ apart............*Persea americana.*

BENZOIN AESTIVALE (L.) Nees. (*Laurus aestivalis* L.) fig. 29. Grains, when moist, nearly or quite spherical, 32–33μ in diameter. Exine extremely thin and transparent, but bearing numerous small deeply staining conical spines, about 2.5μ apart, and very faint lines dividing its surface into polygonal areas, each occupied by a spine at its center. Intine thick and transparent, swelling when moistened to about 4μ in thickness.

This character gives these grains a remarkable resemblance to those of *Heliconia* and allied species and to a lesser extent to those of the Cupres-

sineae and Taxodineae. They may be distinguished, however, from the former by their smaller size, their pointed spines and the fact that the intine instead of presenting a radially striate appearance in optical section, appears to be made up of faintly distinguishable concentric layers. And from the Taxodineae and Cupressineae they are easily distinguished by their small spines instead of the flecks which characterize the latter. When dry these grains shrink without distortion to about 24μ in diameter. The
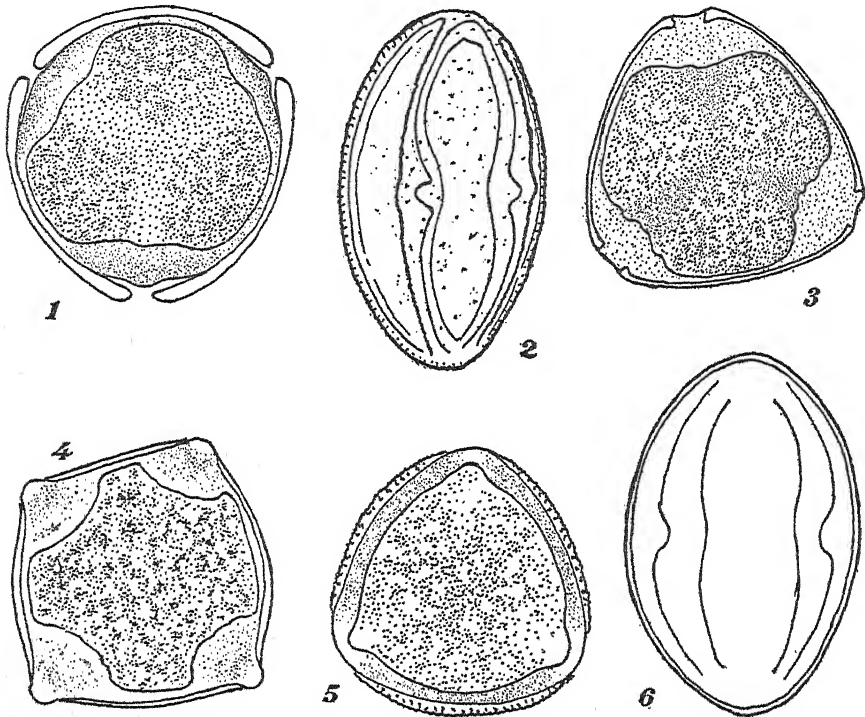
Figs. 1–6. 1. Pollen grain of *Eucalyptus diversicolor*, transverse optical section; 2. Pollen grain of *Rhus glabra*, longitudinal section of a grain that is collapsed and empty; 3. Pollen grain of *Zizyphus Jujuba*, transverse optical section; 4. Pollen grain of *Comptonia peregrina*, a grain with four pores, seen in transverse optical section; 5. Pollen grain of *Ailanthus glandulosa*, transverse optical section; 6. Pollen grain of *Parthenocissus hirsuta*, longitudinal optical section.

major portion of the change is accomplished by the intine for in this condition it measures only about 1.7μ in thickness.

The forms of both this grain and that of *Heliconia* are obviously reduced, and their resemblance to each other is one of the most remarkable examples of convergence I have yet encountered among pollen-grain forms. Since *Heliconia* is a rather typical Monocotyledon, the form of its grain

is presumably derived from the one-furrowed type which characterizes the Monocotyledons. On the other hand since *Benzoin* is a rather typical Dicotyledon, the form of its grain is presumably ultimately derived from the three-furrowed type of grain which characterizes the Dicotyledons. The remarkable form of these two types of grains and that of the Cupressineae and Taxodineae is probably the result of some unexplained environmental stimulus, and deserves further investigation.

PERSEA AMERICANA Mill. (*P. gratissima* Gaert.) Grains essentially as in *Benzoin*. When moist, about 50–64μ in diameter, depending somewhat upon the extent of the expansion of the intine which, when fully expanded, is generally about 15μ thick, considerably thicker than in the grains of *Benzoin*. Spines small, about 4.6μ apart.

A large tree, attaining a height of about 60 feet. Native of tropical America, now much cultivated in California, and to a certain extent in Florida and elsewhere in the warm parts of the U. S. A. for its edible fruit. Insect pollinated. Flowers in spring.

LAURUS NOBILIS L. Grains essentially as in *Benzoin*. When expanded 48–57μ in diameter, depending somewhat upon the extent of the expansion of the intine which is generally about 9μ thick. Spines rather large and each obviously sunk in a little pit (fig. 15), about 5.7μ apart. The exine, though nearly transparent, when properly stained, can be seen to be slightly granular.

A small evergreen tree with stiff leaves and inconspicuous yellowish axillary flowers in early spring. Native of the Mediterranean region. Now much cultivated as a tub plant. The genus contains only one other species which is native of the Canary Islands.

OCOTEA FLAVESCENS Rusby. Grains essentially as in *Benzoin*, 26–30μ in diameter when moist; intine about 3μ thick, spines about 2.3μ apart. A tree about 50–60 feet high, common in mountain forests near Valparaiso.

The genus comprises about 200 species, principally from subtropical America.

CRASSULACEAE

These are mostly herbs and shrubs. There are about 900 species in 20 genera which are of wide distribution and frequently cultivated in rock gardens.

SEDUM L. Grains, when expanded, oblately flattened, rounded triangular in outline when seen in polar view, about 17.1×16μ. Furrows three, situated at the angles of the grain, long and tapering to sharply pointed ends, gaping widely open when expanded. Furrow membranes smooth; germ pore large and bulging prominently out through its germinal aperture. Exine rather thin, but apparently rigid; texture quite smooth. Collapsed grains are ellipsoidal,

about $16 \times 20\mu$, with the furrows tucked tightly into narrow longitudinal grooves through which the pores are scarcely discernible from the surface (fig. 7). Many abortive and dwarf grains are found which are collapsed and measure about $14.8 \times 16.5\mu$.

A genus comprising about 200 species of fleshy herbs, native of temperate and cold regions of the northern hemisphere, Mexico and the Andes of South America.

SEDUM ACRE L. (figs. 18, 20). Grains as in the generic description.

Densely tufted perennial, on rocks along roadsides and in gardens. Native of Europe and northern Asia, but extensively introduced into America. June to August.
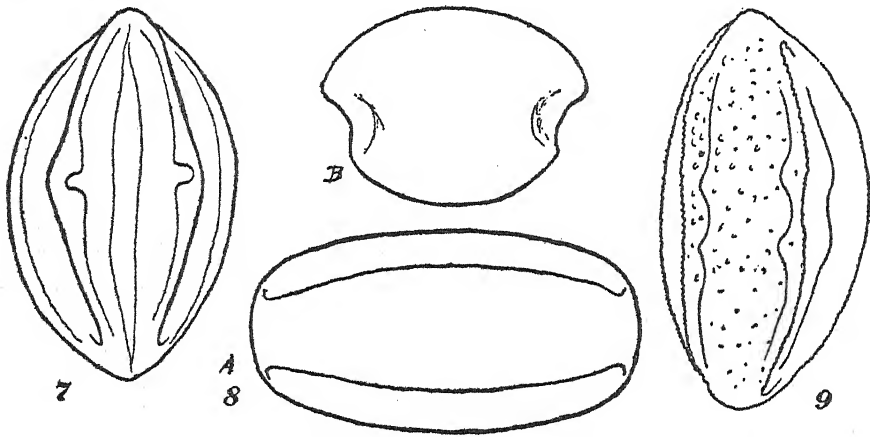
Figs. 7–9. 7. Pollen grain of *Sedum Nuttallianum*, about $16 \times 20\mu$, empty and collapsed, to show the change in form that takes place in *Sedum* grains when the cell contents is dissolved away; 8. Pollen grains of *Pontederia cordata*, diagramatic, A, ventral view and B, end view to show the position of the two furrows; 9. Pollen grain of *Ibervillea Lindheimeri*, optical section of a collapsed grain.

SEDUM NUTTALLIANUM Raf. Grains indistinguishable from *S. acre*, but a small proportion of them show four and six furrows arranged in the trischistoclasic system.

A low tufted annual in dry open places. Mo. to Ark. to Tex. May.

SIMARUBACEAE

There are about 150 species in 30 genera, represented by trees and shrubs of wide distribution in tropical and warm regions.

AILANTHUS GLANDULOSA Desf. (*A. altissima* Swingle). fig. 33. Grains, when moist, oblately flattened, 25–26.5μ in diameter; when dry ellipsoidal, about 20–25.1μ in diameter (fig. 5), tricolpate with long tapering furrows; furrow membranes smooth; germ pores moderately large, circular and clearly

defined. Exine rather thick and coarsely reticulate with the reticulations tending to be linearly arranged.

A rapid-growing tree. Native of China, naturalized in eastern North America, commonly planted as a shade tree. The genus includes about 10 species in Asia and northern Australia.

MALPIGHIACEAE

The grains of the Malpighiaceae are characterized by a tendency towards an increase in the number of their pores and furrows, together with a reduction in their length and definition. All stages may be found from the ordinary tricolpate form with three pores in three well marked furrows, through that with a large number of well developed pores associated with a still larger number of sketchy furrows, to others in which the furrows have entirely disappeared. Such a condition is not unusual in the pollen of other families. It is found in that of the Polygonaceae (Wodehouse '31), and probably represents a stage in the evolution which leads to the many pored furrowless forms, such as those of the Chenopodiaceae and Cucurbitaceae. One outstanding character of the grains of the Malpighiaceae which I have not observed elsewhere, is that the pores tend to be at the ends of the furrows, instead of at the middle.

The family comprises about 650 species of trees, shrubs and woody climbers, of wide distribution in the tropics, particularly the tropical forests of South America, represented in the U. S. A. by *Byrsonima*, *Malpighia*, *Thryallis* and *Aspicarpa*.

I. Furrows clearly defined and generally arranged according to the trischistoclasic system.
   1. Furrows six to twelve, pores 4–6, generally at the ends of the furrows; grain 29–35μ in diameter.
      i. Grains 29–35μ in diameter........................*Heteropterys cornifolia.*
                                            Banisteria leptocarpa.
      ii. Grains 45–58μ in diameter
        a. Furrows generally 12, distinct...............*Gaudichaudia Schiediana.*
                                       Gaudichaudia pentandra.
        b. Furrows various in number, poorly defined....*Gaudichaudia Karwinskiana.*
   2. Pores generally at the centers of their furrows.
      i. Furrows characteristically four.....................*Heteropterys Beecheyana*
      ii. Furrows more than four, various...................*Heteropterys acutifolia.*
II. Furrows entirely absent; pores generally four.............*Heteropterys Gayana.*
III. Furrows present but very irregular and not conforming to the trischistoclasic system; pores 6–12..................................*Malpighia Harrisii.*
                                           Malpighia punicifolia.
                                           Malpighia urens.

GAUDICHAUDIA H. B. K. Grains when expanded almost perfectly spherical, 47–57μ in diameter; when dry, cubical and somewhat smaller, furrows

always 12, excepting in *G. Karwinskiana*, and symmetrically arranged in the ordinary dodecacolpate configuration, shallow, of uniform width throughout their length, rounded at their ends, and with slightly notched or wavy margins; furrow membranes slightly flecked with small granules. Pores six, circular in outline, about 5.7µ in diameter and always at the ends of the furrows which they occupy, and so distributed that there is never more than one pore placed near a triradiate center of convergence, and two of the eight centers are without pores near them. If the grain be so oriented that one of the poreless centers is uppermost, the three furrows which radiate from it each has a pore at its distal end. The other poreless center is exactly opposite on the other side of the grain with its three radiating furrows bearing pores at their distal ends, and alternating with those of the upper center. The remaining six furrows, none of which is occupied by a pore, zigzag across the limb of the grain, converging towards the pores of the two opposite groups. Exine smooth and thin. Intine about 4.5µ thick.

The genus comprises about 12 species of shrubs, commonly climbing, principally in Mexico, with a few in Venezuela and Brazil, though the latter are generally regarded as belonging to the genus *Janusia* Juss.

GAUDICHAUDIA SCHIEDIANA Juss. (fig. 30). Grains as in the generic description, with the furrow pattern always regular and extremely uniform.

Native of Mexico, bearing yellow flowers. Nov.–April.

GAUDICHAUDIA PENTANDRA Juss. Grains exactly as in the type .

Native of Mexico.

GAUDICHAUDIA KARWINSKIANA Juss. Grains mostly similar to the type, but less uniform. Some have furrow configurations corresponding to the dodecacolpate configuration, but with one or more furrows missing and some have larger numbers of pores, up to twelve, introducing various irregularities into their furrow patterns.

Native of Mexico.

HETEROPTERYS Juss. Grains various in the different species.

The genus comprises about 90 species or shrubs, occasionally climbing, principally of southern Brazil and Bolivia, but with a few species ranging northward to Mexico, and a single species, *H. africana*, on the west coast of tropical Africa.

HETEROPTERYS ACUTIFOLIA Juss. Grains various; when moist and expanded, spheroidal, 30–31.5µ in diameter, resembling those of the *Gaudichaudia* type, except in the number and arrangement of their pores and furrows, which are here extremely various. For example there may be 9 furrows and 6 pores, 6 furrows and 5 pores, or 6 furrows and 6 pores. The pores are always at the centers of the furrows which they occupy. Nevertheless the furrows are

generally symmetrically arranged in the trischistoclasic system, though occasionally two furrows may be fused at one or more of the centers of convergence, suggesting in appearance a single long furrow occupied by two pores. Furrow membranes smooth or flecked, margins of the furrows jagged. Pores circular in outline, 2.8–3.4μ in diameter, surrounded by a subexineous thickening which causes them to protrude slightly above the surface of the furrow. Pore membranes smooth; exine rather thick and warty.

A little known species in northern Brazil.

HETEROPTERYS CORNIFOLIA H. B. K. Grains rather uniform; when moist, spheroidal, 28.5–30.5μ in diameter. Furrows generally 9 arranged in the usual nonacolpate configuration, similar in structure to those of *Gaudichaudia*, their membranes granular. Pores generally six and generally at the ends of their furrows, circular in outline, about 5.7μ in diameter, surrounded by an annular thickening which causes them to protrude slightly above the surface of the furrow. Exine smooth or somewhat granular.

HETEROPTERYS BEECHEYANA Juss. Grains similar to those of *H. acutifolia*, but somewhat various, a large proportion abortive and dwarf. Normal grains, when moist, 36.5–40μ in diameter. Furrows always 4, in the ordinary tetracolpate configuration, and with 4 pores which are generally at the centers of the furrows. Furrows of medium length and tapering to sharp pointed ends; germ pores circular in outline, about 6.5μ in diameter, sharply defined and protruding slightly above the surface of the furrow. Exine rather thin.

A shrub in dry savannas, native of Mexico.

HETEROPTERYS GAYANA Juss. Grains somewhat various, with a large proportion abortive; when expanded, spheroidal in form and 36.5–38μ in diameter. Pores 4, circular in outline, each surrounded by a subexineous thickening causing it to protrude rather prominently above the surface of the grain, 3.5–4μ in diameter. Furrows absent. Exine rather thick and warty.

Native of Mexico.

BANISTERIA LEPTOCARPA Benth. Grains similar to the *Gaudichaudia* type, somewhat various and with a small proportion of them obviously abnormal. Normal grains, when moist, spheroidal in form, 32–33.1μ in diameter, when dry they become polyhedral with the furrows lying along the edges, and in this form measure about 30μ in diameter. Furrows mostly 6, 9 and 12, occasionally other numbers, generally beautifully symmetrical in the trischistoclasic system; in form they are very shallow and faint and do not taper towards their ends; their edges are jagged and their membranes flecked with granules. Pores circular, about 7.5μ in diameter, fewer than the furrows, each at the end of the furrow it occupies, and occasionally there are two pores in the same furrow, one at each end. Exine rather thin, finely and faintly granular.

MALPIGHIA L.—Grains similar to the *Gaudichaudia* type, but with a vari-

able number of pores and furrows, the latter often extremely irregular in arrangement, very faint or even altogether lacking.

The genus comprises about 20 species of trees and small shrubs, principally in Mexico and the West Indies, also in the Bahamas and South America to Peru and Brazil.

MALPIGHIA URENS L. Grains spheroidal, 30–33μ in diameter. Furrows very irregular, not arranged in the trischistoclasic system, frequently fused at one or more of their centers of convergence. Pores generally six, circular, 3.4μ in diameter. Exine thin and broken by a number of irregular rifts, sometimes merging with and scarcely distinguishable from the furrows.

Native of the Antilles.

MALPIGHIA HARRISII Small. Grains similar to the preceding, 35–38μ in diameter. "This species appears to be most closely related to *M. urens*." A slender shrub. Jamaica.

MALPIGHIA PUNICIFOLIA L. (*M. biflora* Poir.). Grains spheroidal, 47–53μ in diameter. Pores 6–12 in number, irregularily arranged, 6–8μ in diameter. Furrows entirely absent or represented by faint and irregular markings in the exine which is very thin, possibly too thin to support a clearly defined furrow.

Tropical America.

CELASTRACEAE

The family comprises about 400 species of trees and shrubs or occasionally climbers, distributed throughout the warmer parts of the world.

CELASTRUS SCANDENS L. (fig. 32). Grains uniform, 21–24μ in diameter, spheroidal or slightly flattened, according to the degree of their expansion. Furrows three, sharply defined, long and tapering to slightly rounded ends, their membranes slightly granular, especially around the pores which are rather large and somewhat elongate in the meridional direction. Exine rather heavy and coarsely reticulate.

A climbing shrub with unarmed twining branches, bearing orange and scarlet fruits in autumn; along streams, thickets and fences Que. to Man. south to Ga. Flowers in spring, insect pollinated.

MAYTENUS Molina. Grains uniform, spheroidal, 16–17.1μ in diameter, tricolpate with furrows long and tapering to pointed ends. Furrow membranes smooth, germ pores circular. Exine rather thin, but conspicuously, though finely, reticulate pitted. This grain differs from the *Celastrus* type in its smaller size, finer pitting of the exine and the rounded shape of its pores.

About 120 species of evergreen trees and shrubs, tropical and temperate South America and West Indies. Some species are cultivated for their attactive foliage and fruit.

MAYTENUS ELLIPTICA (Lam.) Krug. & Urb. Grains as in the generic description.

A tree attaining 36 feet, in the forests of Porto Rico.

MAYTENUS TETRAGONUS Griseb. Grains indistinguishable from those of the preceeding species.

Native of the West Indies.

EUONYMUS AMERICANUS L. Grains various, a large proportion irregular, dwarf and abortive. Normal grains generally tricolpate, occasionally tetracolpate, oblately flattened, about 27–31μ in diameter. Furrows long and tapering with their membranes smooth; germ pores round and rather large, about 8μ in diameter. Otherwise similar to the type.

A small to medium sized shrub, partly trailing, on river banks, N. Y. to Ill. Fla. to Ark. Tex. Flowers in summer.

SAPINDACEAE

There are about 125 genera and more than a thousand species of trees and shrubs, often climbing. They are of wide distribution in the tropics and warm regions.

SAPINDUS L. Grains mostly tricolpate, but generally a few with 6 or 9 furrows, somewhat various. Normal grains oblately flattened, 16–20μ in diameter, triangular in outline, with the furrows at the angles. Furrows long and tapering, their membranes smooth and without well defined germinal apertures, the germ pore marked only by a slight swelling. Exine thin, slightly granular or quite smooth.

The genus contains about 15 species of trees and shrubs, native of the tropics.

SAPINDUS MARGINATUS Willd. (fig. 31). Grains as in the generic description.

In low and sandy soil. So. Carolina and Ga. to Fla. Flowers in spring.

SAPINDUS DRUMMONDII Hook & Arn. Grains indistinguishable from the preceding.

In dry soil. Kans. to Ark. La. and Ariz. Also in Mexico. Flowers in spring.

TALISIA Aubl. Grains rather uniform, oblately flattened and somewhat angular in outline when expanded, 21–29μ in diameter, 3- or occasionally 4-colpate with furrows long and tapering, rather vaguely defined, and with their membranes smooth. Germ pores relatively large, elongate in the meridional direction. Exine thin and of smooth texture, merging almost imperceptibly into that of the furrow membrane, so that the boundary of the latter is poorly defined.

About 33 species of small trees in tropical America.

TALISIA OLIVAEFORMIS Radlk. Grains prevailingly 3-colpate, but with a fair proportion 4-colpate, 21.5–23μ in diameter, otherwise as in the generic description.

Yucatan, British Honduras, Colombia, Venezuela and Trinidad.

TALISIA DEPRESSA Pitt. (fig. 27). Grains 3-colpate, rarely, if ever, with higher numbers of furrows, 23.5–28.5μ in diameter. Otherwise as in the generic description. Venezuela.

ANACARDIACEAE

There are about 60 genera and 400 species of shrubs which are most abundant in the tropics.
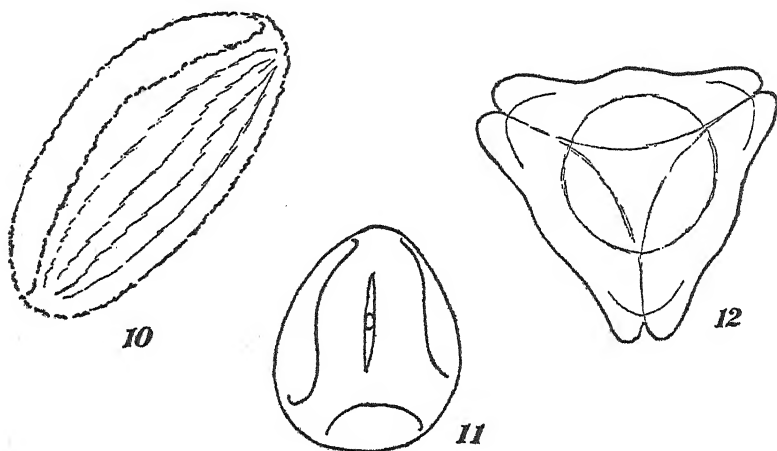
Figs. 10–12. Empty and collapsed pollen grains, as seen by transmitted light, to show their mode of shrinking. It is in such condition that they are most likely to be encountered in fossil material. 10. *Parthenocissus hirsuta*, side view with one furrow showing to the left; 11. *Zizyphus Jujuba*, side view; 12. *Eucalyptus diversicolor*, polar view.

RHUS L. Grains when fully expanded ellipsoidal or spheroidal, 33–39μ broad, tricolpate with long and sharply defined furrows tapering to slightly rounded ends. Furrow membranes slightly flecked with fine granules. Germ pores about 3–4μ in diameter, emerging through a transverse furrow which is sharply outlined by an inwardly projecting ridge. Exine heavy, finely reticulate pitted or occasionally granular. The genus includes about 150 species of trees or shrubs.

Native to temperate, tropical and subtropical regions of both hemispheres.

RHUS GLABRA L. (*Schmaltzia glabra* (L.) Small.) fig. 36. Grains when fully expanded ellipsoidal, 35.3–40μ, when collapsed 25.1×41μ (fig. 2). Exine ex-

tremely finely pitted, sometimes appearing simply granular. Otherwise as in the generic description.

A shrub in dry soil and thickets, N.S. to B.C., Fla. to Miss. and Ariz. Spring and summer.

RHUS TYPHINA L. (*R. hirta* Sudw., *Schmaltzia hirta* (L.) Small.) Grains spheroidal or slightly ellipsoidal, 37.5–39 μ in diameter. Exine finely but conspicuously reticulate. In these two characters easily distinguished from the type.

A shrub or small tree in rocky soil. N. B. to Ont. Minn. Ga. and Miss. Spring and summer. Insect pollinated but shedding large quantities of pollen.

SPONDIAS MOMBIN L. (*S. lutea* L.) Grains similar to the *Rhus* type, long ellipsoidal, 34–39μ broad and 43–50μ long. Furrows long and tapering to sharp pointed ends. Furrow membranes smooth or only very slightly flecked with granules. Germ pore 8μ in diameter, broader than the furrow and forcing it apart as it bulges through, but not provided with a transverse furrow. Exine coarsely reticulate pitted, with the pits elongate and linearly arranged in a meridional direction. This grain is easily distinguished from that of *Rhus* by its more elongate form, the coarser pitting of the exine and absence of transverse furrows.

A tree attaining 25 feet in height. Tropical America. Frequently cultivated.

RHAMNACEAE

The family comprises about 600 species in 50 genera, of trees and shrubs of wide distribution.

ZIZYPHUS JUJUBA Lam. (*Z. sativa* Gaert., *Z. vulgaris* Lam.) figs. 3, 35. Grains decidedly flattened and triangular in outline, 21.5–23μ in diameter, with their germinal apertures, one at each angle. Pores elliptical, 3.4μ long, elongate in the meridional direction; tricolpate, but the furrows are represented by only very shallow streaks which are frequently scarcely visible. Each pore is surrounded by a weakly developed subexineous thickening which gives it an aspidate appearance. Exine thin and smooth.

A shrub or small tree, native of southern Europe, and southern and eastern Asia. Cultivated elsewhere.

ZIZYPHUS SONORENSIS Wats. Grains indistinguishable from the type.

A shrub, native of Mexico.

VITACEAE

The family comprises about 500 species in 12 genera, mostly tendril-climbing woody vines, though there are also included in it some erect

shrubs and even small trees. Principally of the tropics and warm temperate regions.

PARTHENOCISSUS HIRSUTA (Donn) Graebn. figs. 6, 34. Grains, when expanded, $30 \times 40\mu$. Tricolpate with furrows long and tapering; furrow membranes smooth, provided with well marked germinal apertures, 4.6μ broad. Exine thick and conspicuously reticulate, with the network most open towards the centers of the lunes, closer towards the poles and along the margins of the furrows.

A spreading, tendril-climbing vine. Ga. to Tex. and Mexico. Spring.

PARTHENOCISSUS QUINQUEFOLIA (L.) Planch. (*Ampelopsis quinquifolia* (L.) Michx.) Grains essentially the same as the type, except that they are somewhat less elongate.

A strong high-climbing woody vine. Native of eastern North America. Spring. The genus comprises about 12 species of woody tendril-climbers, Native of North America and Asia.

VITIS VINIFERA L. Cultivated Grape. Grains extremely irregular and various in form and size. Normal grains $19–22\mu$ in diameter, prevailingly tricolpate, but a large proportion have 4 or 6 furrows, either regularly arranged in the trischistoclasic system, or variously irregular. Furrows poorly defined, their membranes smooth; germ pores round. Exine very thin, much thinner than in the grains of *Parthenocissus*, but faintly reticulate.

STERCULIACEAE

The family includes about 750 species in 10 genera, of plants of all forms, throughout the tropics of both hemispheres. It is of particular interest because it contains *Theobroma Cacao*, the source of chocolate, and *Cola acuminata*, the Cola Nut.

STERCULIA L. Grains always uniform, slightly ellipsoidal to spheroidal, depending upon their degree of expansion, about $30.4 \times 33.5\mu$; tricolpate with furrows sharply defined, long and tapering, their membranes flecked with granules. Germ pores sharply defined and somewhat elongate in a transverse direction. Exine very coarsely reticulate but with low ridges.

About 60 species of trees in the tropics of both hemispheres, but mostly in the East Indies and Malay Archepelago.

STERCULIA APETALA (Jacq.) Karst. (*S. carthaginensis* Cav.) fig. 23. Grains as in the generic description.

Tropical America.

STERCULIA MEXICANA R. Br. Grains indistinguishable from the type. Mexico.

STERCULIA FOETIDA L. Grains indistinguishable from the type. Cuba.

TERNSTROEMIACEAE

There are about 175 species in 16 genera of trees and shrubs, native of tropical and subtropical regions throughout the world.

TERNSTROEMIA GRANULATA Kr. & Urb. (fig. 22). Grains uniform, ellipsoidal when expanded, 16–18.2μ in diameter; tricolpate with furrows long and tapering, their membranes smooth. Germ pores large, bulging prominently through their apertures, about 5.5μ in diameter. Exine thin and perfectly smooth. A small tree, native of Jamaica. May–Sept. with white fragrant flowers.

The genus, also known as *Taonabo* Aubl., comprises about 30 species of evergreen trees and shrubs in tropical America and Asia.

PROTEACEAE

The family comprises about 1000 species in 50 or more genera, of trees and shrubs, native of Australia, South Africa, tropical eastern Asia and tropical South America.

LOMATIA ILICIFOLIA R. Br. (fig. 26). Grains decidedly flattened and triangular or triradiate in outline, about 33μ in diameter, with three pores without furrows, each situated at the end of a horn-like projection. Germinal apertures approximately circular in outline; pore membrane generally provided with a single central fleck. Exine lightly marked with a very slightly raised reticulum.

LOMATIA OBLIQUA R. Br. Grains indistinguishable from the type.

A shrub or small tree native of Chile.

BANKSIA L. f. Grains always uniform, two-pored, elongate and arched, with one pore at each end, about 51×24.5μ. Pores circular, about 8μ in diameter, surrounded by a slightly thickened collar of the exine. Exine smooth or faintly granular.

The peculiar form of these grains with their projecting germ pores, as compared with those of *Lomatia,* suggests that this form may be a two pored derivative from the *Lomatia* type. They further differ, however, in their smooth texture and larger size.

This unusual and striking form of pollen grain, besides being common to the two species of *Banksia* here described, according to Francis Bauer[4]

[4] Francis Bauer, F.R.S. 1758–1840. Drawings of about 215 species of pollen grains, unpublished, are deposited in the British museum (Natural History). The majority of these are in the form of unfinished sketches, though a few are beautifully finished in natural colors. He appears to have left no notes, other than their names and occasional brief descriptive sentences to facilitate the completion of the drawings, but these, together with the drawings, both completed and unfinished, show an understanding of pollen grains many years in advance of his time.

also characterizes that of *Banksia media, B. Cunninghamia, B. marginata, Dryandra floribunda* and *D. formosa*. It thus appears that this grotesque form is firmly established in the family, and is not due merely to some individual or specific anomaly in the arrangement of the pollen cells in their tetrads as the form suggests. Its origin in relation to tetrad formation, certainly deserves further study.

The genus comprises about 45 species of trees and shrubs, exclusively Australian. Flowers extremely small, 500 to 1000 tightly compacted in a large brush-like head.

BANKSIA CANDOLLEANA Meissn. (fig. 21). As in the generic description. Sand plains of western Australia.

BANKSIA PROSTRATA R. Br. type. Grains as in the type, except that their form is slightly more arched, and their exine slightly more granular, especially around the pores.

MYRTACEAE

The family comprises about 3000 species in 72 genera, of trees and shrubs, native in the tropics, particularly of America and Australia.

EUCALYPTUS L'Her. Grains rather uniform, except for a large proportion that are abortive, generally flattened and triangular in outline, about $25 \times 19\mu$. Germinal furrows three, one at each angle, extremely short, each consisting of an elongate and rather vaguely defined depression in the exine with its major axis directed meridionally; it is crossed by a rather conspicuous transverse furrow. The area where the latter underlies the former constitutes the germinal aperture and is rather small. Neither the pore nor the furrow of these grains functions in accommodating volume changes. This function is obviously taken over by the flattened polar surfaces which by becoming more or less arched can easily compensate for any increase or decrease in size. The pores are surrounded by a rather conspicuous subexineous thickening which gives them an almost aspidate appearance. Exine rather thick and perfectly smooth.

The genus comprises about 300 species of mostly tall trees, native of Australia and the Malayan region.

EUCALYPTUS DIVERSICOLOR F. M. (fig. 25) type. Grains as in the generic description.

A tall tree native of western Australia, cultivated in California.

EUCALYPTUS ROBUSTA J. E. Smith. Grains essentially as in the type.

A tall tree, cultivated in California.

ARALIACEAE

There are about 500 species in 50 genera, herbs shrubs and trees of wide distribution.

ARALIA SPINOSA L. (fig. 24). Grains when moistened decidedly flattened and triangular in outline, 25–30μ in diameter; when dry they tend to become more flattened and more triangular; tricolpate with furrows of medium length and tapering to sharp points. Furrow membranes always ruptured when expanded, marked by a faint centrally placed granular streak. Germ pores large and bulging prominently Exine rather thick and conspicuously reticulate but somewhat finer towards the margins of the furrows.

A tall shrub or tree attaining a height of 30 ft. So. Pa. to Mo. and Fla. "Frequently planted for the oddity of its thick club-like branches" which suggest its English name Hercules Club. The genus comprises about 40 species of herbs, shrubs and trees, native of Asia, Malaya, Australia and North America.

CAPRIFOLIACEAE

The family comprises about 350 species of trees shrubs and vines, principally of the north temperate zone, a few in the mountains of the tropics.

SAMBUCUS L. Grains uniform, spheroidal or somewhat ellipsoidal, depending upon the degree of their expansion, 17–26μ in diameter, tricolcolpate, with furrows very long, in one species sometimes meeting at the poles, their membranes smooth, each with a large bulging germ pore with poorly defined margins. Exine conspicuously reticulate throughout, except towards the margins of the furrows where it merges with their smooth membranes, with slight differences in the different species.

The genus comprises about 20 species of shrubs and small trees in temperate and subtropical regions of both hemispheres.

SAMBUCUS CANADENSIS L. (fig. 28) type. Grains as in the generic description, about 18μ in diameter; furrows of medium length, not joined at the poles. Exine finely reticulate.

A large shrub producing cymes of showy white flowers in June and July. N. S. and Man. to Fla. and Tex.

SAMBUCUS PERUVIANA L. Grains essentially as in the type, about 21.6μ in diameter. Exine more coarsely reticulate.

Shrub, native in tropical and subtropical America.

SAMBUCUS NIGRA L. Grains similar to the type, about 17.1μ in diameter. Furrows frequently all three, or sometimes two of them, united at the poles. Exine finely reticulate.

A shrub or tree sometimes 30 feet high, bearing yellowish flowers in late spring. Native of Europe.

CUCURBITACEAE

These are annual or perennial succulent herbs, usually trailing or climbing by means of tendrils; about 700 species in 90 genera; mostly of tropical regions around the world, but some species extending into temperate zones.

IBERVILLEA LINDHEIMERI (Gray) Greene. fig. 9. Grains, when expanded, approximately spherical, about 59μ in diameter, tricolpate with furrows long and tapering to somewhat rounded ends. Exine thick, finely reticulate pitted.

Slender climbing or trailing herbs. In valleys, Tex. to so. Calif. Spring to fall. The genus comprises about 8 species of perennial vines in Mexico and southern U. S. A.

LUFFA ACUTANGULA Roxb. (*L. foetida* Cav.). Grains spheroidal, about 86μ in diameter, tricolpate with medium-long tapering furrows; furrow membranes flecked with a central streak of granules. Pores rather small, circular or elliptical in outline with their major axis directed meridionally. Exine apparently covered with fine bristles, in this respect bearing some resemblance to that of *Cucurbita*.

A strong vine, in cultivation in America and escaped in tropical America. The genus comprises 7 or 8 species, native of the Old World tropics.

CUCURBITA PEPO L. (type). Grains uniform, spherical, $130–145\mu$ in diameter, without furrows but with about 10 large circular pores, $20–27\mu$ in diameter. Each pore is provided with an operculum adorned with numerous short bristles and one or two long sharp spines, resembling a spiked helmet. The arrangement of the pores over the surface of the grain is not isometric, but approaches the tasithynic, suggesting that the pores represent reduced furrows. Intine rather thick and rigid. Exine covered with closely packed bristles giving it a granular appearance, also provided with many large sharp spines. With the highest magnification these are seen to be uniform shafts of homogeneous material, standing at right angles to the surface, about 6.5μ long, sharply pointed at their summits and flaring at their bases but approximately cylindrical through their central part. They are beautifully symmetrical in their arrangement which is almost exactly isometric.

The species exists in cultivation in many varieties, including such forms as the bush pumpkin, summer squash and yellow-flowered gourds. The genus includes about 10 species of annual or perennial trailing herbs, probably all American.

LAGENARIA LEUCANTHA Rusby (*L. vulgaris* Ser.). Grains in general form similar to the type, $160–190\mu$ in diameter. Germ pores 9–12 in number and 30–

35μ in diameter. Spines of the exine 6.5μ long, but narrowed at the base instead of flaring as in the type. Surface of the exine appears to be finely granular, but may be composed of tightly packed bristles as in the type.

The genus contains but a single species, a variable long-running annual; native of the Old World tropics, but now wide-spread in warm countries, and in cultivation represented by many varieties such as the dipper and calabash gourds.

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YONKERS, N.Y.

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Explanation of plates

All figures were drawn from studies made at a magnification of 900, using a Zeiss 3 mm. apochromat objective, N.A. 1.4, and paired 15 × binocular eye pieces. Measurements, except those of very large grains, were made at a magnification of 1800, using 2 mm apochromat objective, N.A. 1.3, and a 20 × eye piece. The sizes of the drawings are chosen to best display the characters of the grains and do not bear a constant relation to their sizes. The measurements given are those of average dimensions.

PLATE 20

Fig. 13. Pollen grain of *Sparganium androcladum*, about 23μ in diameter, showing its coarsely reticulate surface and single germ pore.

Fig. 14. Pollen grain of *Heliconia Bihai*, about 80µ in diameter, showing the thin transparent exine bearing numerous warts, and the thick transparent intine surrounding the cell contents, the darkened central globe.

Fig. 15. A single spine from a grain of *Laurus nobilis*. These are slightly larger than those of *Benzoin* (q.v., fig. 29, Pl. 22), otherwise exactly the same.

Fig. 16. Pollen grain of *Comptonia peregrina*, about 27µ in diameter, with three pores, seen in side view.

Fig. 17. Pollen grain of *Pontederia cordata*, about 48µ in length, side view showing one of its two furrows; the other furrow is exactly opposite. The dorsal surface is towards the left and is connected with the ventral surface, towards the right, by two narrow isthmuses, one at each end of the grain (cf. fig. 8).

Fig. 18. Pollen grain of *Sedum acre*, about 17×16µ, side view.

Fig. 19. Pollen grain of *Brasenia Schreberi*, about 57µ in length, side view, showing its single asymmetrical furrow.

Fig. 20. Pollen grain of *Sedum acre*, polar view, cf. fig. 18.

PLATE 21

Fig. 21. Pollen grain of *Banksia Candolleana*, about 51×24µ. Its two germ pores are seen one at each end of the grain.

Fig. 22. Pollen grain of *Ternstroemia granulata*, about 17µ in diameter, side view.

Fig. 23. Pollen grain of *Sterculia apetala*, about 30×33µ, side view.

Fig. 24. Pollen grain of *Aralia spinosa*, about 30µ in diameter, polar view.

Fig. 25. Pollen grain of *Eucalyptus diversicolor*, about 25×19µ, polar view, showing its short pit-like furrows.

Fig. 26. Pollen grain of *Lomatia ilicifolia*, about 33µ broad, polar view, showing its triradiate flattened form and reticulate surface.

Fig. 27. Pollen grain of *Talisia depressa*, about 28µ in diameter, transverse optical section.

Fig. 28. Pollen grain of *Sambucus canadensis*, about 18µ in diameter, side view.

PLATE 22

Fig. 29. Pollen grain of *Benzoin aestivale*, about 33µ in diameter, showing its thin transparent exine bearing numerous conical sharp spines, and thick transparent intine.

Fig. 30. Pollen grain of *Gaudichaudia Schiediana*, about 55µ in diameter. A triradiate center of convergence of furrows is uppermost and slightly to the right. There is another such triradiate center on the opposite side but with its furrows alternating with those of the upper center. Altogether there are 12 furrows.

Fig. 31. Pollen grain of *Sapindus marginatus*, about 18µ in diameter, polar view.

Fig. 32. Pollen grain of *Celastrus scandens*, about 23µ in diameter, polar view.

Fig. 33. Pollen grain of *Ailanthus glandulosa*, about 26µ in diameter, polar view.

Fig. 34. Pollen grain of *Parthenocissus hirsuta*, about 30×40µ, side view.

Fig. 35. Pollen grain of *Zizyphus Jujuba*, about 22.5µ in diameter, polar view showing the three furrows which are merely slight depressions in the exine.

Fig. 36. Pollen grain of *Rhus glabra*, about 37µ in diameter, side view.

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WODEHOUSE: GREEN RIVER POLLEN
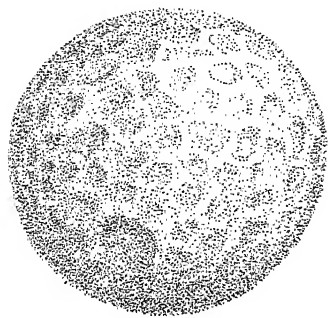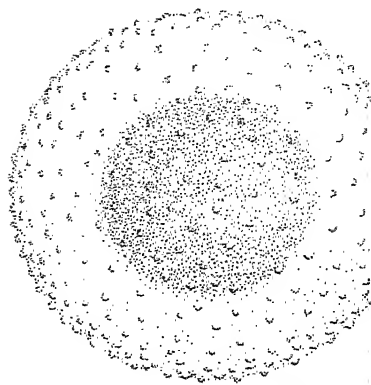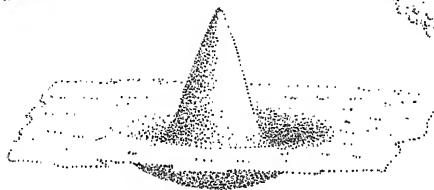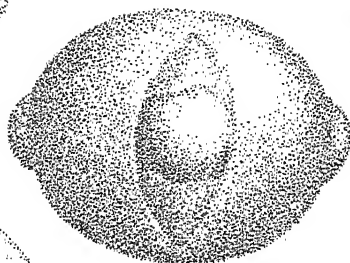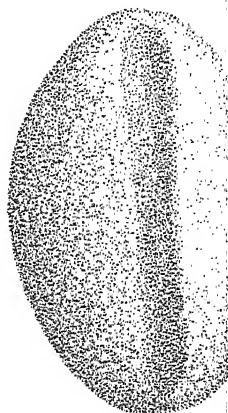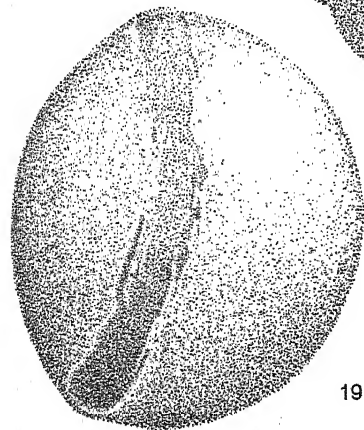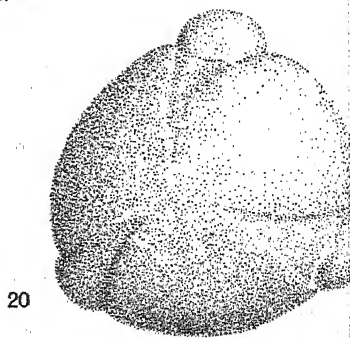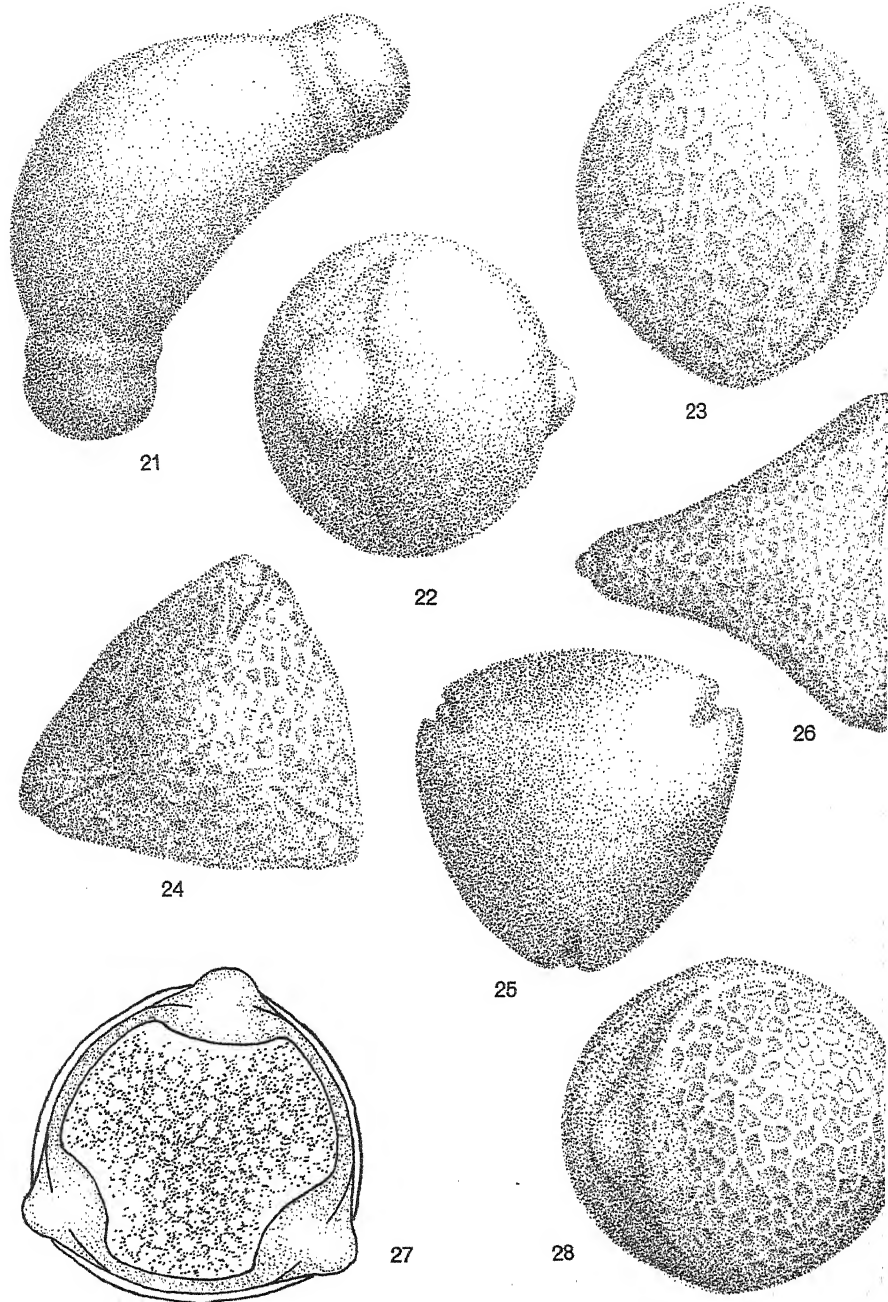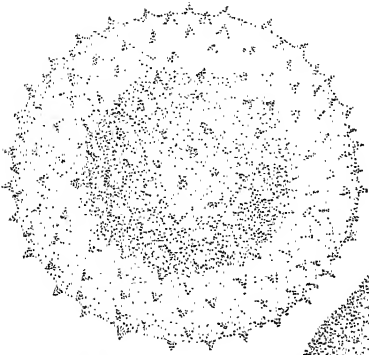
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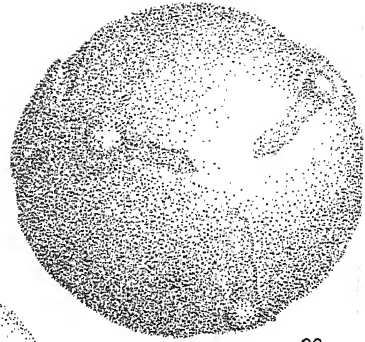
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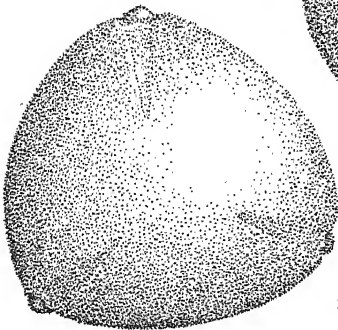
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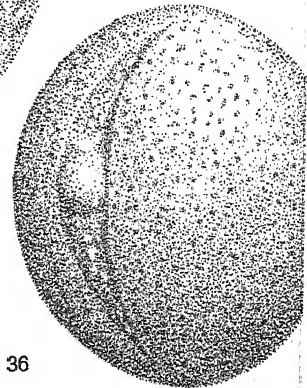
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An hermaphroditic self–sterile but cross-fertile condition in Pleurage anserina[1]

L. M. AMES
(WITH ONE TEXT FIGURE)

Much thought has been given to the sexuality of the fungi in late years. The discovery of heterothallism in the Mucorales by Blakeslee, and subsequently in the Ascomycetes, Eubasidiomycetes, rusts and smuts by other investigators, has stimulated intensive interest in this subject which at the present time is receiving great attention especially in the rusts and in the Ascomycetes. The present interest concerning this condition in the fungi goes back to the pioneer work of Blakeslee who obtained experimental evidence for heterothallism in the Mucorales by isolating and growing single spore cultures which by themselves produced only asexual spores, but which when certain of them were mated together produced rows of zygospores along the lines of intermingling hyphae. On this basis (Blakeslee, A. F. 1904. Sexual reproduction in the Mucorineae. Proc. Am. Acad. Arts and Sci. 40: 205–319. *pl. 1–4*) he interpreted heterothallism in relation to sex as follows: "The assumption that their differentiation to (+) and (−) strains was indicative of a corresponding sexual difference, and that the strains thus designated should be regarded respectively as male and female, or vice versa, although naturally suggested by the observed condition, did not at first appear to be warranted. Evidence, however is not lacking which would seem to justify such a conclusion." With this evidence and with additional data Blakeslee established the fact that in certain of the Mucorales heterothallism involved the fact that there was present in one mycelium the potentiality of only one sex. Because heterothallism involving uni-sexuality was thus established in certain cases in the Mucorales, it has become the generally accepted view that heterothallism and uni-sexuality in the fungi are synonymous terms. Although this assumption has been found to be an adequate explanation for the sexual condition in certain species of fungi, it seems natural to suppose that other conditions may exist.

The writer working with *Pleurage anserina* (Ces.) Kuntze has found a sexual condition which modifies the conception of sexuality as outlined above, and offers a different interpretation of the sexual condition in this fungus. Previously the writer (Ames, L. M. 1930. A study of some homothallic and heterothallic Ascomycetes. Mycologia 22: 318–322) had reported a homothallic condition in this fungus as the result of work done with single spore cultures from normal bi-nucleate ascospores which occur four in an ascus. At that time, also, the writer had observed that occasional

asci contained either more or less than the normal number of spores, for example now and then asci contained three normal bi-nucleate spores and two small uni-nucleate spores. At that time, however, the sexuality of the small uni-nucleate spores was not determined.

Meanwhile E. Silver Dowding (Dowding, E. Silver. 1931. The sexuality of the normal, giant, and dwarf spores of *Pleurage anserina* (Ces.) Kuntze. Ann. Bot. 45: 1–15. *pl. 1+f. 1–10.*) reported that mycelia derived from dwarf uni-nucleate spores of *Pleurage anserina* were heterothallic, and in the same article she pointed out also that the mycelium from the normal ascospore bore no kind of secondary spore, stating: "The mycelia bore neither oidia nor any other kind of secondary spore which might be a source of contamination of the cultures."

During the fall of 1930, however, the writer while working on cultures derived from these small uni-nucleate spores of *Pleurage anserina* and studying the compatibility of strains derived from these uni-nucleate spores by pairing them in all possible combinations, discovered that in addition to the coiled ascogonia (see text fig. 1), from which the perithecial fundaments develop, there were produced on short branches of the mycelium minute spherical spores (microspores) (see text fig. 1) which functioned as spermatia, and this involved a situation very different from that usually conceived of as heterothallism. Many single spore cultures were made and each was found to produce the two types of sex organs just mentioned. These cultures derived from single uni-nucleate spores, by themselves, never produce perithecia, even though both the ascogonia and spermatia are present and have every opportunity for self-fertilization because they are growing intermingled (see text fig. 1). However, when the mycelia of many single spore cultures are mated together in pairs in all possible combinations so that the spermatia of one have opportunity to fertilize the ascogonia of the other, it is found that approximately 50 per cent of such crosses produce perithecia, while in the other 50 per cent of the crosses the perithecial fundaments never complete their development. Subsequently, the writer using two strains found to be compatible, had no difficulty in artificially fertilizing the ascogonia of one with the spermatia transferred from the second, and the ascogonia of the second with the spermatia transferred from the first (see text fig. 1). Perithecia were developed in all cases only in the immediate area where the spermatia were placed.

In connection with these experiments on cross-fertilization it was noted that the spermatia never produced mycelia nor germinated on nutrient substrata. Spermatia, under observation both in Van Tieghem cells and on several different types of nutrient agar, swelled several times in volume,

CULTURE A:
HERMAPHRODITIC. SELF-STERILE

BUT
CROSS-FERTILE
IN EITHER DIRECTION
♂A TO ♀B
♂B TO ♀A

CULTURE B
HERMAPHRODITIC SELF-STERILE

FERTILIZATION   SELF-STERILE   SELF-STERILE   FERTILIZATION

AMES
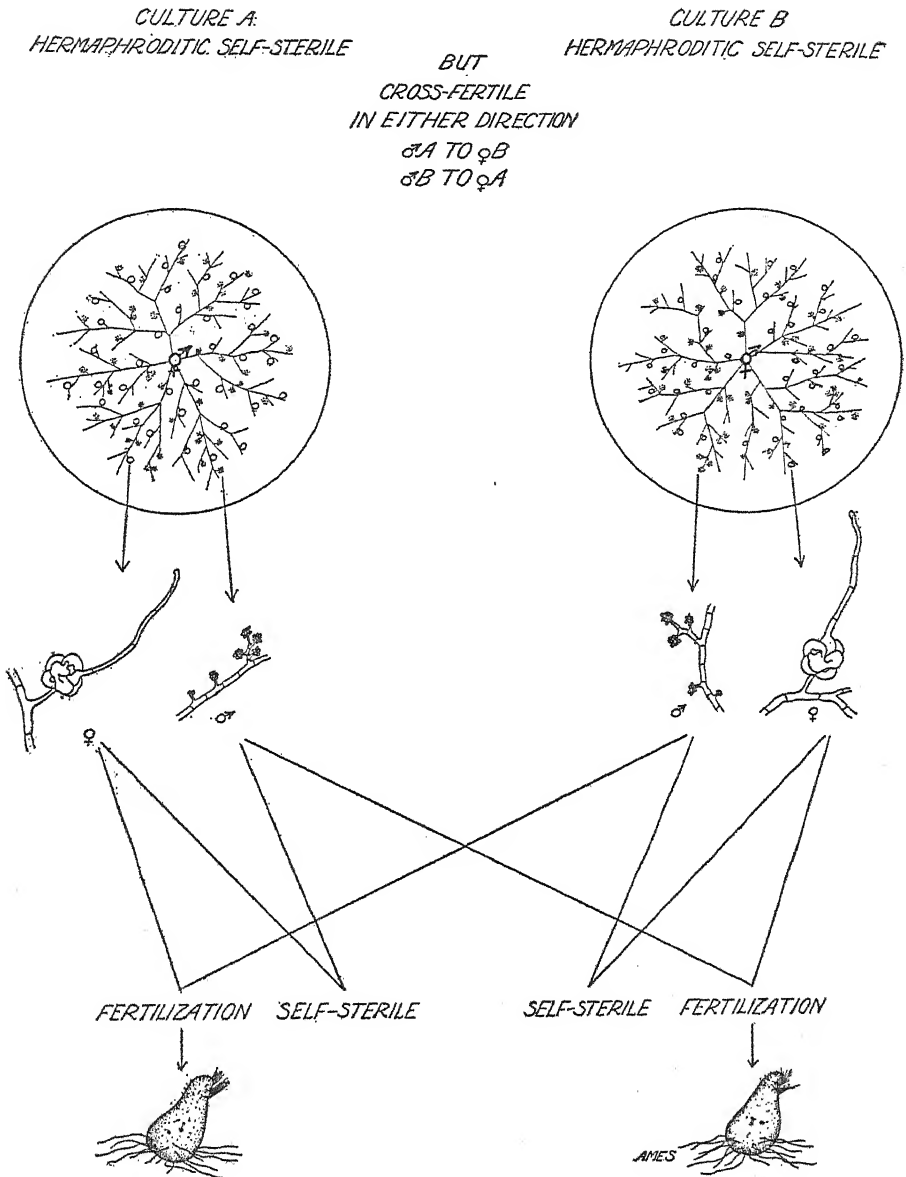
Fig. 1. Diagrammatic representation of the sexual condition in the hermaphroditic self-sterile strains derived from the uni-nucleate ascospores of *Pleurage anserina*, and of the production of perithecia by cross-fertilization of compatible strains. The young ascogonia are drawn from a photomicrograph and are in proportion to the size of the spermatia.

but beyond their increase in size no further development has been noted even after several weeks under conditions apparently suitable for germination and under the same conditions in which fertilization took place. However, when spermatia are placed on compatible ascogonia the development of these into perithecial fundaments was discerned with the unaided eye even within as short a time as seventy-two hours. This fact indicates that the nuclei of the spermatia enter the trichogyne of the ascogonium very soon after the spermatia come in contact with the trichogyne, and the cytological details of this are now being worked out.

Inasmuch as some investigators have found that injury to mycelium in the case of certain Fungi Imperfecti induces sporulation at the place of injury, it seemed necessary to prove that possible injury in transferring the spermatia was not responsible for the development of the perithecial fundaments. Therefore lacerations of the mycelium of similar cultures were made with sterile transfer needles, and in no case did such injury stimulate any perithecial development.

The writer, therefore, is driven to the conclusion that the ascogonia, which are abundant on all of these cultures from single, uni-nucleate spores, develop into perithecia only after being fertilized by compatible spermatia. The strains from uni-nucleate ascospores of *Pleurage anserina* are therefore not heterothallic strains, male and female respectively, but are hermaphroditic self-sterile strains, requiring cross-fertilization by compatible opposites for the production of mature perithecia.

The writer is continuing this work and from observations recorded above, together with additional data, feels justified in drawing the following conclusions:

1. In *Pleurage anserina* the mycelia derived from small uni-nucleate ascospores are in reality hermaphroditic strains, self-sterile, but capable of cross-fertilization if compatible.

2. Each monosporous culture derived from dwarf, uni-nucleate spores develops both male and female organs; small spermatia (microspores) and large ascogonia with coiled trichogynes.

3. These male and female organs on mycelia derived from monosporous cultures of the dwarf spores are self-sterile.

4. Cross-fertilization by transferring compatible spermatia from one culture to another results in the formation of mature perithecia from the ascogonia thus fertilized.

5. Injury to the mycelium by sterile transfer needles does not stimulate the production of perithecia.

6. The non-production of mycelium from the spermatia together with

their effect in cross-fertilization indicates that they do not function as conidia, but as true spermatia.

7. Between compatible single spore strains successful cross-fertilization of the ascogonia of one with the spermatia transferred from the second, and the ascogonia of the second with the spermatia transferred from the first, demonstrates that the male and female organs are each functional.

LABORATORIES OF CRYPTOGAMIC BOTANY
HARVARD UNIVERSITY

The non-sexual and the sexual functions of microconidia of Neurospora

B. O. DODGE

(WITH PLATES 23, 24 AND ONE TEXT FIGURE)

I have previously[1] reported that certain albinistic strains of *Neurospora sitophila* produce microspores of the type formed by *Botrytis* and *Sclerotinia* as figured by Woronin. These microconidia germinate to produce mycelia which appear to differ in no way from mycelia derived directly from ascospores or from monilioid conidia. Furthermore, races 56.2 and 56.6, which are of opposite sex in their reactions[2] both produce such microspores. It was stated in the paper referred to that the mycelia derived from these races could be mated to produce perithecia. I have been reminded, however, that it was not stated that these mycelia could be *mated together*. This opportunity is taken to make this point clear as requested, and to report some further work along the same line. As a check on my own culture work, I have asked my assistant, Miss Marjorie E. Swift, who has acquired an excellent technique for isolating very small spores through her work on *Penicillium* and other fungi, to repeat my work on microconidia. Much additional evidence supporting certain statements included here resulted from her careful work.

Humphrey[3] states that microconidia of *Sclerotinia fructigena* of the Woronin type germinated in his cultures and produced normal mycelia. His descriptions of the process and the accompanying figures are rather convincing even though others have questioned his work. My own one attempt to obtain germination with microspores of *S. fructigena* also resulted in failure.

Brierley[4] has reported (he has in a recent letter positively confirmed that report) that microconidia of *Botrytis cinerea* germinate freely to pro-

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[1] Dodge, B. O. Breeding albinistic strains of the *Monilia* bread mold. Mycologia 22: 9–38. 1930.

[2] Is it necessary to explain again that I always use the terms "sex" and "opposite sex" simply for convenience until someone tells us just what it is that sets off the mechanism which regulates perithecium formation. A good term for this condition is needed. To quote from one of my other papers[11]: "In this paper the terms hermaphroditic, homothallic, haplomonoecious and bisexual are all used in the same sense to indicate a mycelium having two kinds of nuclei as to their sex, *or whatever it is here that corresponds to sex.*"

[3] Humphrey, J. E. On *Monilia fructigena*. Bot. Gaz. 18: 85–93. 1893.

[4] Brierley, W. B. The microconidia of *Botrytis cinerea*. Kew Bull. Misc. Information 1918: 129–146. *pl. 5.* 1918.

duce normal *Botrytis* mycelia. There can be no doubt, from his account of the way these microspores are formed, that they are entirely different from the ordinary conidia which characterize the genus *Botrytis*. Are they morphologically spermatia, homologous with the microconidia of *Sclerotinia* as figured by Woronin? Whether these little bodies germinate or not, the germination test will be the basis for the conclusions which will be reached by those who hold that *function* determines homologies.

The microconidia of *Neurospora* are, as stated in the paper referred to[1], apparently formed in much the same way that they are in *Botrytis* and *Sclerotinia*, except that instead of arising on bottle-shaped "sterigmata" they form directly from individual cells of the branched microsporophore. (In several species of *Sclerotinia* microspores also arise in much the same way directly as buds on the surface of the macroconidia and ascospores as well as from the cells of germ tube hyphae without evident sterigmata.) They are not formed internally as endospores, yet they appear as though forced out through a collared opening, one after another, occasionally adhering in a little chain for a short time. This collar structure may, however, represent a very short sterigma. The illustrations (text fig. 1, a-f) show about what one sees under oil immersion magnification. Figure 1, g, is taken from Brierley's paper on *Botrytis* for comparison. Plate 23, a, b, shows the branched microconidiophores, under various magnifications. Professor R. A. Harper, and others who were kind enough to examine my preparations, were satisfied that these structures are true microconidia and not small monilioid conidia. They are to be compared with the microconidia of *Sclerotinia*. At c (plate 23) are seen numbers of microconidia at the time they were sowed for germination, and at d, equally magnified, a few of the same bodies about 40 hours later, when some of them had germinated. They always do germinate on corn meal agar if given two or three days to do so. It is necessary to exclude all monilioid conidia and mycelial fragments, otherwise the plate will be overgrown before the microspores have a chance to germinate.

When one accidently sows an old detached microsporophore along with the microspores it does not sprout out as would an ordinary mycelial branch. It lies on the surface of the agar unchanged for a long time (for at least 80 hours as was observed in one case). In the meantime microspores all around it will have germinated and grown out branched systems of hyphae. Of course if it is still attached to its parent hypha, the hyphal cells may sprout within a few hours and ruin the experiment. It may be that even the old cells of the microsporophore would eventually send out hyphal branches if left long enough, particularly if one that had produced only a few microspores were tried out. If the microspore is still attached

it will germinate and give the appearance of a cell sprouting. There is no reason, except complete differentiation, why a young microsporophore branch should not sprout out vegetatively. After the whole crop of micro-spores has been produced, that would naturally leave the individual cells exhausted. These microsporophores and the little "spores" which they pro-duce are certainly curious structures. I shall show later on that the micro-spore can perform another function which supports the theory that in their morphology they represent ancestral male elements. When they germinate as described above, however, they are simply reverting to perform a vege-tative function.

The production of microspores is not confined to the non-conidial albinistic races. Race Arl.10.42 which produces monilioid conidia, also
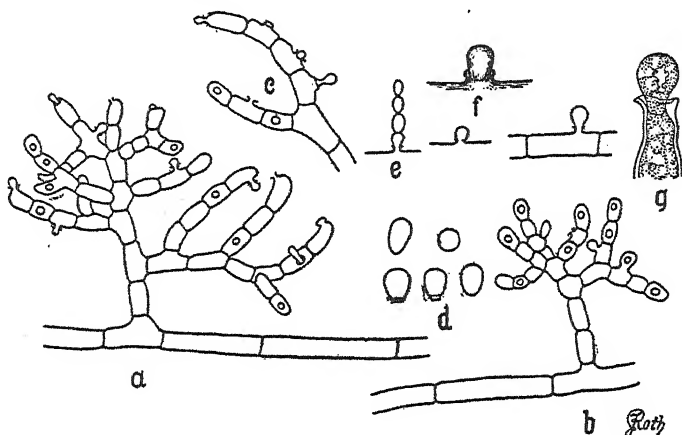
Fig. 1, a–f. Origin of microconidia in *Neurospora sitophila*. Various magnifications. The little circle in a cell is to represent a surface view of the collar-like projection from which microspores arise. Several cells show a side view of this collar. g. Sterigma and microconidium of *Botrytis cinerea*, after Brierley.

forms microconidia. Strains S_1 and S_6, of *N. tetrasperma* produce both kinds of conidia. Furthermore, certain normal conidial races of *N. crassa* which were examined in plate cultures, were found to be producing microspores rather abundantly. The photographs (plate 23, e-g) show that the microconidiophore may be either unbranched (e) or, even dichoto-mously branched (g). At f, lower center, are seen two microspores as they arise from adjacent cells. Microspores of *N. crassa* are usually ovoid to pear-shaped, and slightly brownish in color. They are formed just as they are in *N. sitophila* and *N. tetrasperma*, and germinate in the same slow way. Mycelia from microspores derived from pure conidial races produce monilioid conidia and microconidia in turn.

MATING MYCELIA DERIVED FROM MICROSPORES

Starting with the non-conidial races 56.2 and 56.6, which are haplonts A and B, and of opposite sex in their reactions, a number of single-microspore cultures were isolated. Some 20 matings of these cultures resulted in an abundance of mature perithecia in each case (plate 24, e). When the first set of single-microspore cultures had produced microspores in turn, a second generation set of cultures was obtained. Again twenty matings were made between pairs of mycelia obtained from the second generation of microspores. In every case, again, an abundance of perithecia matured. This confirms fully the assertion[1] that these microspores germinate like true spores and their mycelia are perfectly normal, showing the same type of sexual reaction as that of the parent mycelia from which the microspores were obtained. Because of their very small size they are probably, in general, uninucleate. This gives us a better opportunity to study such somatic segregations as occur in cultures. Ordinary monilioid conidia contain several nuclei, and therefore mutations are more likely to escape notice.

Another line of cultures was started from strain Arl.10.42, which also produces a few monilioid condia, and it so happened that the microspore isolates in this case turned out to be non-conidial[5]. The microspore isolates from a good conidial race of *N. crassa*, however, produced an abundance of conidia.

The theory that the ascomycetes and basidiomycetes have been derived from the red alga line has been much strengthened within the past few years. Professor R. A. Harper in reviewing Rosenvinge's work on *Phyllophora brodiaei*[6] before a group of botanists recently, pointed out how perfectly this alga parallels a typical ascomycete in its morphological features. Unintentionally, because he does not even mention the fungi, Svedelius[7], in his discussion of lines of evolution within the red alga group, has made it easier for mycologists to see how these algae and the ascomycetes are very similar in their organization.

[5] Strain Arl. 10 is the unstable parent strain (see reference in footnote no. 1) from which, by plating out the monilioid conidia one can obtain races such as Arl. 10.42 which produce very few monilioid conidia. When I refer to a race as non-conidial it is meant that it produces no monilioid conidia. It may or it may not produce microconidia in any particular culture.

[6] Rosenvinge, L. K. *Phyllophora brodiaei* and *Actinococcus subcutaneus*. Det. Kgl. Danske Videnskab. Selskab. Biol. Middelelser. VIII. 4: 1–40. 1929.

[7] Svedelius, N. Nuclear phases and alternation of generation in the Rhodophyceae. Beih. Bot. Centralb. 48: 38–59. 1931.

Very recently it was my privilege to read in advance of publication a preliminary paper by F. L. Drayton[8] on "The sexual function of the microconidia in certain discomycetes." He reports that in *Sclerotium Gladioli* the microconidia function the same as do the "pycniospores" of the rusts; that is, he "spermatizes" certain receptive structures with non-germinating microconidia of his *Sclerotium*, with the result that apothecia of the genus *Sclerotinia* are developed in his culture. He would argue on this basis that microconidia are male in their morphology and function, and that: "It is highly probable that this sexual mechanism is operative, with perhaps slight modifications in all spermatia-producing Ascomycetes . . . ." This would certainly be the very best kind of evidence that the red algae were the ancestors of our higher ascomycetes.

"SPERMATIZING" WITH MONILIOID CONIDIA (N. TETRASPERMA)

Unreported experiments demonstrated before a group of university students a few years ago may be of interest in this connection. Race S_1 (*N. tetrasperma*, haplont B) was grown in one petri dish and race S_6 (haplont A) in another for a few days, or until the mycelia had covered the plates. The monilioid conidia from S_1 were then sowed in a drop of water on two or three different spots on plate S_6, and vice versa. The drop of water is quickly absorbed by the agar and disappears. A few days later perithecia were formed over small areas where the drops of water carrying the monilioid spores had been placed.

This experiment has been repeated recently. The results show beautifully how one can "spermatize" with ordinary monilioid conidia. Plate 24, f, (the two upper spots), shows such a result from "spermatizing" with ordinary conidia. The two lower spots will be referred to in another connection.

It will, of course, be said that when these conidia are laid on a spot in a drop of water, they germinate quickly and produce mycelia which react in the same way that any two mycelia of "opposite sex" react, whatever way that may be, to produce perithecia in a culture. Evidence that this is probably not the case is furnished by an interesting experiment. A plate was inoculated with race S_6 on one side, and another plate was inoculated in the same way with race S_1. After the mycelia had grown part way across the plates in each case, monilioid conidia from S_1 were placed on a marked spot at the tip ends of hyphae in plate S_6, and monilioid conidia from S_6 were placed in a similar position in plate S_1. The plates were then incubated

[8] Drayton, F. L. The sexual function of the microconidia in certain discomycetes. Mycologia 24: 345–348. 1932.

for four days. During this brief period perithecia had begun to develop rapidly on the marked spot in plate S_1, and the original mycelium in the plate had grown out to the edge of the culture. This is an illustration of successful spermatization with macroconidia. (For a similar picture see Plate 24, c.)

Quite a different picture was presented in the other culture (Plate 24, a). What had happened is easily understood, and it throws much light on the question as to just what is going on in both cases. S_6 race is a rather slow-growing race, so that the conidia of S_1, being in contact with fresh agar medium at the tips of the S_6 hyphae, germinated normally and grew out rapidly in the only direction not already occupied by the oncoming hyphae of race S_6, that is, away from the hyphal tips. Spermatization could not occur because the conidia had already germinated to form hyphae. One could see on the second day how the S_1 hyphae were spreading out in a broad fan-like growth, always keeping out beyond and around the more slowly growing S_6. The photograph shown in Plate 24, a, gives the picture seven days after the conidia from race S_1 had been placed on the spot marked by the circle at x. The curved line marks the limit of hyphal growth at the time spermatization was attempted. The culture in which spermatization of S_1 by monilioid conidia from S_6 was successful presented a picture like that shown at c in Plate 24, although this is a picture of another culture to be described later. One can successfully spermatize a culture of race S_6 with conidia from race S_1 if he places the conidia on the mycelium back of the hyphal tips, or say, at y (see Plate 24, a) instead of at x as was actually done in the experiment. This has been done several times and perithecia usually appear on the marked spot within 48 hours if the culture is not an old one. The experiment in which macroconidia were placed on mycelia of the opposite sex as described here was originally suggested by another of somewhat different nature.

Races S_1 and S_6 were grown in separate plates as before. After about ten days a small block of agar from S_1 now covered with hyphal growth etc. was put in plate S_6, and vice versa. The results were quite different, though perithecia were formed in both cases. Where the block of S_6 agar was laid on S_1 plate, the perithecia were formed on the S_6 block and not on the agar in the S_1 plate. Where the block of S_1 was laid on plate S_6 the fruit bodies were formed on the S_6 agar in the plate, not only directly under the little S_1 block but for some distance away on all sides. This behavior may not hold in all cases, but here, at least, it looked as though the S_1 were the more potent spermatizing or diplodizing agent. This is quite the opposite of the conclusion one reaches when he observes the results obtained in the experiments on spermatizing the microconidia described below.

"SPERMATIZING" WITH MICROCONIDIA (N. TETRASPERMA)

The experiment on "spermatizing" noted above was repeated recently but microconidia instead of monilioid conidia were used. At the same time the experiment was checked by using monilioid conidia for "spermatizing" at other points. Strains S_1 and S_6 were grown as before in separate petri dish cultures. After three days, or when the mycelia had covered the plates, microspores were taken from S_6 and placed in drops of water on marked spots on plate S_1. At the same time macroconidia in drops of water were placed on other marked spots on the same plate. Four days later perithecia had begun to develop in all cases, not only where the microconidia were used for spermatization, but also where the monilioid conidia were used. Plate cultures of S_6 were also successfully spermatized with macroconidia from S_1, but microspores of the latter were not available at the time.

There are two conditions that bear on the success of these experiments. First, the mycelium to be spermatized should not be too old. Several attempts to stimulate perithecium formation in cultures two weeks old resulted in failure. Second, in order to spermatize successfully the microspores should be obtained from fairly fresh cultures, cultures only a few days old. Microspores from cultures 25 days old, on the other hand, germinated well when sowed on sterile agar plates. This would seem to indicate that although age may be an inhibiting factor in spermatizing, germination of the microspores is not seriously affected. Further work along this line is desirable.

"SPERMATIZING" WITH MICROCONIDIA AND MONILIOID CONIDIA (N. SITOPHILA)

Albinistic non-conidial races 56.6 and 56.2 were grown separately three days in plate cultures. Microconidia from the 56.6 line were used to spermatize plate 56.2 at certain marked spots, and microconidia from the 56.2 line were used to spermatize plate 56.6 at certain spots. As a check and for comparison monilioid conidia from the normal conidial race 56.3 were used to spermatize plate 56.6, and monilioid conidia from race 56.8 were used to spermatize plate 56.2 at certain marked spots. The plates were then incubated at about 25°C. for only forty-eight hours when perithecia began to show on each of the marked spots in every case except where the microspores from line 56.6 had been placed on plate 56.2. Perithecia developed on these spots also, however, hours later (Plate 24, b). Since under similar conditions the microspores, if placed on corn meal agar and incubated, would have just begun to germinate after forty-eight hours, we may assume that at least the microsopores actually functioned as spermatia, passing their nuclei on to whatever receptive organs are involved.

The macroconidia of *Neurospora sitophila* seem to function equally well as "spermatizing" agents, just as was proved to be the case in *N. tetrasperma*. Each of two agar plates was inoculated on one side with the non-conidial race 56.6. After forty-eight hours the mycelium had grown about half way across the plate in each case. A line was drawn on the bottom of the plate to mark the limits of growth. Macroconidia from race 56.3 were placed on a marked spot in one plate so that some of the conidia were in contact with the hyphal tips. Microconidia from race 56.2 were placed in like manner on the other plate. The cultures then incubated for forty-eight hours. By the end of this time the original mycelia had overgrown both plates and perithecia were already showing in both cultures but only on the marked spots which had been spermatized (Plate 24, c, d). No doubt perithecia could have been detected several hours earlier had the cultures been examined. When 56.2 is spermatized either with microspores from race 56.6 or with macroconidia from race 56.8 it requires a longer time for perithecia to develop, and there are, for some reason, not so many of them.

One can reverse the experiments described above by growing conidial races in plate cultures for a day or two and then spermatizing with microspores on some spots, and with macroconidia on other spots. For example, when conidial race 56.3 was spermatized with microspores of 56.6, and on other spots with macroconidia of race 56.8 many perithecia developed after about sixty-four hours. Cultures of conidial race 56.8 were spermatized in like manner with microspores of race 56.2 and on different spots with macroconidia of race 56.3. Perithecia were plentiful on all of the spermatized spots in this case also at the end of sixty-four hours. When mycelia of these conidial races of opposite sex reaction are grown together in tube cultures it usually requires five or six days before perithecia begin to show.

SEXUAL VERSUS NON-SEXUAL FUNCTIONS

Holding that the theory of origin of the ascomycetes from the red algae is the more plausible one, it must be conceded that there was no doubt as to the facts in the case when reporting phenomena[1] (germination of microconidia) that may well be interpreted to support the opposing theory, namely, that the ascomycetes have arisen in a monophyletic line from the oomycetes. Now, Drayton says that his microconidia function the same as do the "pycniospores" of the rusts, and adds that the few cases where germination of microconidia of ascomycetes is reported, remain to be satisfactorily explained. Just how do the "pycniospores" of the rusts function? Some say they germinate, but Andrus[9] alone, of those who

[9] Andrus, C. F. The mechanism of sex in *Uromyces appendiculatus* and *U. vignae*. Jour. Agr. Res. **42**: 559–589. 1931.

have been studying this question recently, says positively that they do not germinate. They are true spermatia, he says, and function as such by passing their nuclei on to trichogynes or trichogynous hyphae. Whatever may be the way the pycniospores of the rusts and the microconidia of *Sclerotium Gladioli* function, we do know that when microspores of *Neurospora* germinate to form mycelia, which, when properly chosen, can be *mated together* to produce perithecia, they are not functioning solely as male organs or spermatia. They are functioning as true spores. One can claim however, that they actually perform their spermatium function when afforded an opportunity to provide the impulse for perithecium formation, that is, when one "spermatizes" with them. The zoosporangia of certain species of the Peronosporales under particular conditions of moisture and temperature germinate like ordinary conidia to produce infection tubes. Zoospores of *Synchytrium* can reinfect the host directly, or they can function as gametes and fuse in pairs, male with female, but often showing merely relative sexuality, as in case of *Ectocarpus*.

There is a very intriguing theory which was briefly stated by Kniep[10]. A rust like *Puccinia Helianthi* is in fact hermaphroditic or haplo-monoecious, and not heterothallic. Each mycelium produces male elements, spermatia, and also something else that functions as a female element. We are misled into thinking that it is heterothallic because it is necessary to cross-spermatize to obtain aecia. Kniep says this may be nothing but a form of self-sterility determined by factors which segregate according to the mono-hybrid scheme. Had he known at the time that each mycelium of *Neurospora* also produces microspores in addition to ascogonial coils and sterile perithecial bodies, he would, no doubt, have applied the same line of reasoning to account for the results to be obtained by mating pairs of mycelia each of which is by itself sterile. (In one of my earlier papers[12] it was stated that: "Mycelia of species of *Neurospora* produce coiled structures which very likely are morphologically sex organs. . . . The two mycelia which are opposite in their reaction in the production of perithecia have been classified provisionally as haplonts A and B.") Gwynne-Vaughan and Williamson[13] have since reported that all races of heterothal-

[10] Kniep, H. Die Sexualität der niederen Pflanzen. Jena. 1928. See pp. 454, 455.

[11] Dodge, B. O. Inheritance of the albinistic non-conidial characters in interspecific hybrids in *Neurospora*. Mycologia 23: 1–50. 1931.

[12] Dodge, B. O. Production of fertile hybrids in the ascomycete *Neurospora*. Jour. Agr. Res. 36: 1–14. 1928.

[13] Gwynne-Vaughan, H. C. I. & H. S. Williamson. Contributions to the study of *Humaria granulata*, Quel. Ann. Bot. 44: 127–145. 1930.

lic *Humaria granulata* produce oogonia. Gregor[14] and Buisman[15], working independently, have reported on two species of *Ceratostomella* which are heterothallic, yet monospore cultures in all cases produce incipient perithecia and small asexual spores. *Sclerotium Gladioli* is still another example of the same sort, and Drayton[8] has, for the first time, in a convincing manner, demonstrated that the microspores can be made to function in "spermatizing" certain receptive organs to the end that apothecia are matured. Kniep points out[16] that one could assume with Correns in accounting for the reactions of our so-called heterothallic ascomycetes that each haploid mycelium contains potentialities of both male and female sexes, but that there are genes, "determinators," that impress on such a mycelium either a male or a female stamp when it comes to the origin of fruit bodies.

All of which is just another way of saying that the genes or factors that determine the primary sex function are not indissolubly linked with those factors regulating the development of ascogonial coils, perithecial frameworks, and spermatia (microspores). Or, to put it another way, a monospore mycelium of *Neurospora sitophila* is, to all intents and purposes, unisexual when it comes to sexual reproduction. As long as this gene or determinator does not weaken, that mycelium must react as, say, the male parent only. As yet the results of hundreds of tests have not brought to light any strain of *N. sitophila* derived from a single ascospore from an 8-spored ascus that would produce perithecia *with asci* without being mated in culture with some other strain. The discovery of such a strain is highly desirable, as it would serve to confirm Kniep's (Correns') theory for the rusts as applied to the ascomycetes like *Neurospora*. I am inclined to accept this theory in principle, in spite of the fact that the microspores in *Neurospora* can germinate and produce normal mycelia, because they can also be used to spermatize directly.

Why must the mycelium derived from a microspore be male, just because we may insist the microspore is homologous with the spermatium. In its sexual reaction the mycelium from a microspore or spermatium must be exactly like the mycelium that produced that microspore. The latter mycelium got all its elements of inheritance from a single ascospore nucleus. Segregation and distribution of genetic factors occurs just previous

[14] Gregor, M. J. F. A study of heterothallism in *Ceratostomella pluriannulata* Hedgcock. Ann. Myc. 33: 1–9. 1932.

[15] Buisman, C. *Ceratostomella ulmi*, de geslachtelijke vorm van *Graphium ulmi* Schwarz. Tijdschr. Plantenz. 38: 1–8. 1932.

[16] Kniep, H. Vererbungserscheinungen bei Pilzen. Bibliographia Genetica 5: 371–478. 1929.

to ascospore formation at reduction, and not at "spermatogenesis," if we may refer to a microspore as a spermatium and the process of its formation as spermatogenesis.[17] A microconidium has, barring somatic segregation or mutation, all the potentialities of a monilioid conidium, all the potentialities of an ascospore, all of the potentialities of the whole mycelium for that matter. If you give a microspore the right cultural conditions there is no fundamental reason, except its small size, why it should not germinate. We naturally want to see the microspore pass on its nucleus without showing signs of germination to make it a good spermatium. In "spermatizing" with conidia it may be necessary for them to thin out the wall a little by going through the first stages of germ tube formation. If one grows S_1 mycelium of *N. tetrasperma* opposite S_6 in a petri dish culture[11], just to take one case for an example, it looks more as though the S_6 were being "diplodized," as Professor Buller would say, rather than spermatized, because the perithecia seem to be formed on the S_6 mycelium alone, the fruit bodies being placed more or less along the lines of mycelial growth of that haplont. According to the Correns-Kniep theory each mycelium of the pair is reacting as of one sex only. That is to say, as long as the "determinator" does not weaken, S_6 is the female parent only, here. This may possibly be true in the experiments with S_1 and S_6 previously described (p. 352) but it would not be easy to answer objectors who would insist, but without any proof, that, since one can spermatize equally well regardless of which mycelium of the pair furnishes the microspores, either mycelium, or both in the same culture, can act as the female parent.

No amount of speculation or theorizing on the nature of sex in the ascomycetes will alter the fact that one can breed and hybridize strains and species of *Neurospora* just as though he were dealing with unisexual races. If we leave out the idea of maleness and femaleness the old word

[17] In *Drosophila* spermatogenesis connotes or involves reduction division and segregation of certain genetic factors, whereas in *Neurospora* the formation of spermatia involves not segregation but only differentiation or coming to maturity. If one will cut off a young ascogonial coil of *Neurospora* and plant it in a culture medium, and if it buds at all, it will grow out into a normal mycelium which in turn will produce microspores as well as ascogonia. The reason why the microsporophores did not bud out to form mycelia in the experiments previously described was probably because they were not tried out until they were too old, or had become exhausted through the production of masses of microconidia. The development of antheridial branches as distinct from oogonial branches in *Pyronema* is a case of sex differentiation and not sex segregation. It is a coming to maturity of the mycelium. If one could cut off the antheridial branch very early in its growth it would no doubt bud out to form a normal mycelium which would produce both ascogonia as well as antheridia in turn. Whether any particular ascogonial or antheridal branch will become vegetative when excised will depend upon to what extent differentiation has already occurred.

heterothallism is still a good one, because the two mycelia that must be grown together to produce perithecia are different, although we do not know just how they are different. My results with *Neurospora* throw further light on the questions that might be raised with respect to the implications in my former papers,[18] namely, that self-perpetuating androgenetic, parthenogenetic, and syngamic (hermaphroditic) races exist in the blackberry rust.

Very interesting examples of the working out of incompatibilities were frequently encountered in the experiments on breeding interspecific hybrids previously described,[11] especially among the hermaphroditic hybrids. In the latter cases it was not difficult, by separating out the unisexual components, to prove that the incompatibility was quite aside from the question of sex. Whether sex as it works out in *Neurospora* is in the same category with sex of a pollen grain, a sperm, or an egg cell, may be a question. If it is not, it is a perfect substitute and it is regulated in the same way.

We have a four-spored species of *Neurospora* obtained from Dr. R. A. Toro in Porto Rico. It has behaved rather peculiarly. Single ascospore cultures produce perithecia abundantly, so that it is hermaphroditic, and it corresponds morphologically to *N. tetrasperma*. When the unisexual component strains of the Toro species were mated against S_1 and S_6, which are *N. tetrasperma* unisexual tester strains, no perithecia were formed in either case. Toro's species does not seem to hybridize readily with our *N. sitophila* and *N. crassa*, although in all these cases one can tell, by the reactions, when mycelia of opposite sex are being paired. This is an illustration either of interspecific sterilities or geographical incompatibilities. What species the Toro fungus really represents, is still an uncertainty. It behaves as though it were a different species altogether from the three we have in culture, even though morphologically it is like *N. tetrasperma*. By working out such forms as this we shall unquestionably arrive at a better understanding of what we mean by sex as well as what constitutes a species in these fungi.

After page proof of the above was received further data on the development of perithecia through spermatization have been obtained. In two plate cultures of *Neurospora sitophila*, strain 56.6, forty-eight hours old, "sclerotia" were visible only within about $1\frac{1}{2}$ centimeters from the original

[18] Dodge, B. O. Uninucleated aecidiospores in *Caeoma nitens* and associated phenomena. Jour. Agr. Res. **28:** 1045–1058. 1924; Cytological evidence bearing on the sexuality and origin of life cycles in the Uredineae. Proc. Internat. Congr. Plant Sci. 1926: 1751–1766. 1929. Dodge, B. O. & L. O. Gaiser. The question of nuclear fusions in the blackberry rust, *Caeoma nitens*. Jour. Agr. Res. **32:** 1003–1024. 1926.

point of inoculation. The mycelium had grown practically across the plate in each case. Monilioid conidia of strain 56.3 were placed on a marked spot showing many sclerotia about half a centimeter from the inoculation point. A drop of water without conidia was placed on a corresponding spot in the other plate. Twenty-two hours later perithecia had begun to develop on the marked spot. None showed on the control. This provides further evidence that the monilioid conidia had functioned as spermatizers rather than as spores which germinated.

At the margin of growth where no sclerotia were visible at the time, monilioid conidia of 56.3 were placed in a marked area on one plate and check was provided by placing a drop of sterile water on a similar marked spot in the other plate. Twenty-seven hours later many perithecia began to show on the spermatized spot. Whether this difference of five hours represents the time required for the development of the necessary receptive structures is a question to be answered by later experiments.

On page 352 (Plate 24, a) an experiment was described showing the difference between the results obtained when macroconidia function as spermatizers and when they function normally as spores producing mycelia. This experiment has since been checked by using microspores instead of monilioid conidia. It has been shown that if the microspores are first allowed to germinate to produce small mycelia before coming in contact with a mycelium of the opposite sex, then the perithecia which are produced are distributed as they are in every case where two mycelia of opposite sex are grown in the same culture. That is, they are distributed progressively over wide portions of the plate, whereas if the microspores are placed directly on a mycelium of the opposite sex, then they act as spermatizers and the perithecia are confined largely to the spot over which the drop of water containing the spores spread at the time of spermatization.

THE NEW YORK BOTANICAL GARDEN
NEW YORK CITY

Explanation of plates

PLATE 23

a–d. *Neurospora sitophila;* e–g. *N. crassa.* Various magnifications.

a. Microconidiophores under low power; b. The central cluster from figure a; c. Microconidia just as sown on agar surface; d. Some of the same microspores about 40 hours later when germination was well under way, the same magnification as those shown in c; e. Unbranched microsporophore showing two little chains of microspores; f. Oval, pear-shaped, to elliptical microconidia. At lower center note two microspores as they arise from adjacent cells; g. Dichotomously branched microsporophore of *N. crassa,* microspores attached to parent cells, seen along the sides of the branches.

PLATE 24

a. *Neurospora tetrasperma.* The mycelium of race S_6 had grown out to the line on the second day after inoculation. Monilioid conidia from race S_1 were then placed on the spot marked *x.* Spermatization was not successful because these conidia had time to germinate. The new mycelium grew out rapidly and perithecia were formed in the usual way at the end of the fifth day. If the conidia had been placed on spot *y* back of the tip ends of hyphal growth, successful spermatization would have occurred and perithecia would have covered the spot, and not have been distributed widely as shown in this picture.

b. *N. sitophila,* race 56.6. Spermatization was effected with macroconidia on the two upper spots and with microconidia on the two lower spots. Perithecia appeared in all cases after 48 hours.

c. *N. sitophila,* race 56.6. Mycelium allowed to grow two days when it reached the line. Macroconidia from race 56.3 were then placed on the spot marked by the circle. Within the next 48 hours many perithecia developed as a result of successful spermatization with macroconidia.

d. Same as c except that microspores from race 56.2 were used for spermatization. Perithecia appeared on the spot after 48 hours.

e. Plate culture inoculated on opposite sides with mycelia derived from second generation microspores obtained from races 56.2 and 56.6 respectively. Perithecia developed on the mycelium of the 56.6 race.

f. *N. tetrasperma.* After 3 days mycelium of S_1 was spermatized on the two upper spots with macroconidia from race S_6, and on the two lower spots with microspores from race S_6. Perithecia developed on all the spots after 4 days.
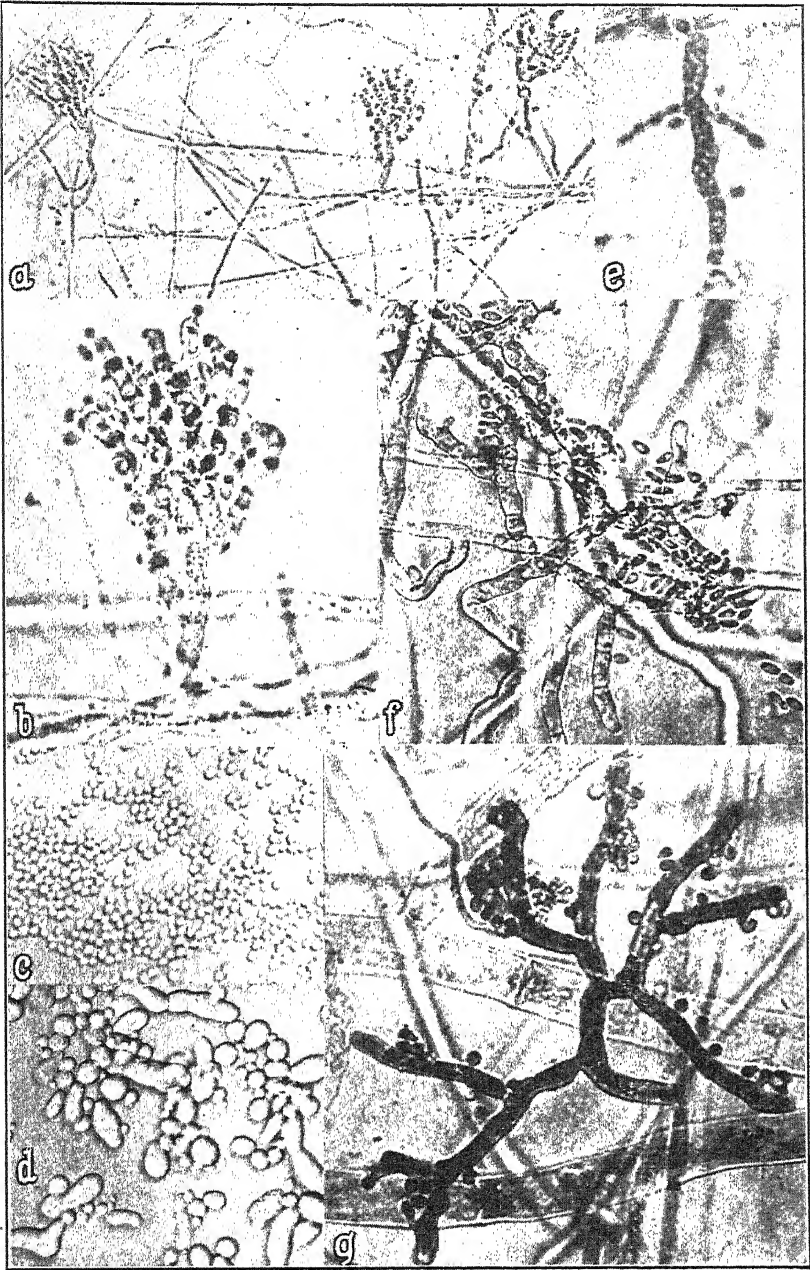
DODGE: NEUROSPORA

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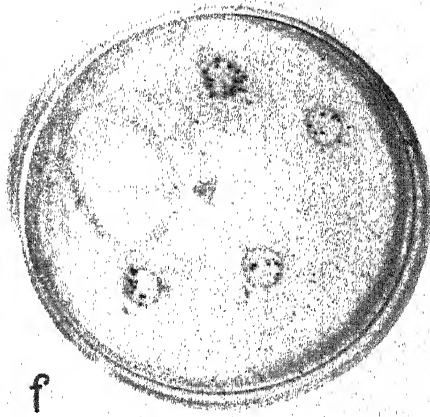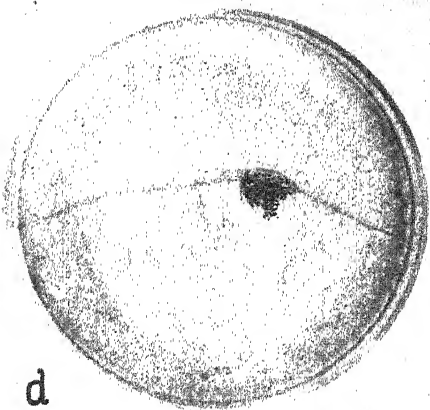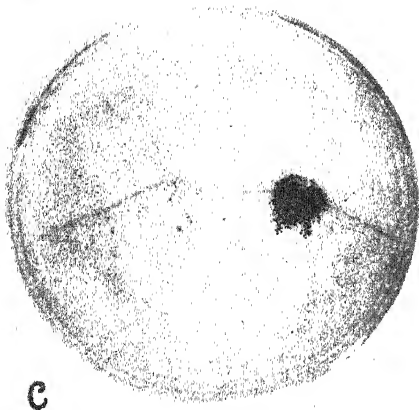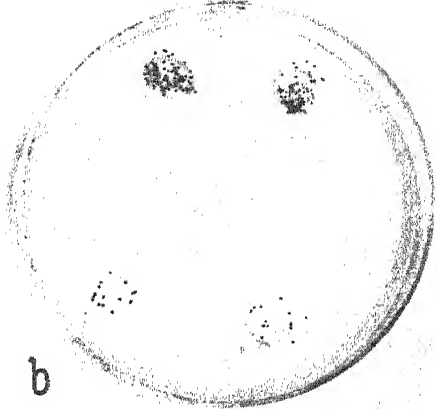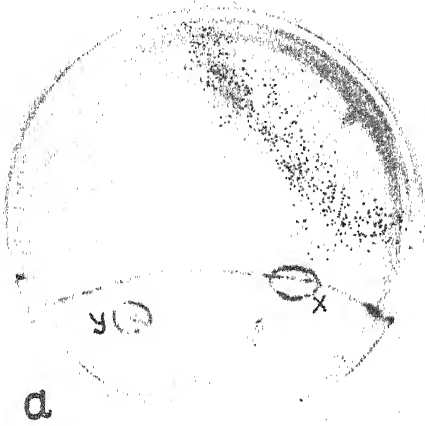
Studies on the flora of northern South America—XVII.

H. A. GLEASON

A GROUP OF SPECIES IN MICONIA SECTION JUCUNDA

The section *Jucunda* of the great genus *Miconia* contained twelve known species in 1891, according to Cogniaux in his monograph of the family Melastomataceae. Since that time two others have been described, *M. involucrata* Donn. Sm. of Guatemala and *M. polita* Gl. of British Guiana, so that the section embraces to date fourteen species, while two additional species are described below. As a section, *Jucunda* is not well distinguished from *Tamonea*, its chief feature being the well developed triangular sepals, in contrast with the short sepals or scarcely developed calyx-lobes of *Tamonea*.

When representative material of this section is brought together, it is at once seen that eight of the species possess a number of common characters and form in themselves a compact species-group. So distinctive are these characters and so unlike those of other species of *Miconia* that the student of the genus is led to the conclusion that these plants represent a phylogenetic group of closely related species. The leaves are ample and pli-nerved. The flowers are sessile in small clusters subtended by conspicuous bracts (in *M. gratissima* the clusters are looser and the bracts probably smaller than in the others; I have never seen material in good flowering condition). The hypanthium is tubular and more slender than in most species of the genus. The ample calyx is deciduous at the torus at or soon after anthesis. The sepals are ovate or triangular and connivent or even connate in bud. In all except *M. holosericea* each sepal is prolonged into an unusually large and conspicuous exterior tooth, usually triangular in cross-section and completely concealing the sepal proper; in the excepted species the exterior tooth is merely a thickened protuberance. In five of the other seven species the free margin of the sepal proper is greatly reduced or lacking and may be easily overlooked, while in the last two, *M. acuminata* and *M. francavillana*, the true sepals are narrowly triangular or linear and about equal the exterior tooth in length. The pollen-sacs, together with a branch of the connective, are separated basally and prolonged below the insertion of the filament; the connective often bears a dorsal protuberance near its base. The ovary is a third to a half inferior, or even almost free. These floral characters are scarcely evident until the flower is dissected. On the herbarium sheet the exterior teeth invariably conceal the true sepals and may easily be mistaken for them.

The species may be separated by the following key:

Leaf-blades acute or cuneate at base, on petioles 1–3 cm. long.
  Exterior tooth a minute thickening, about equaling the rounded tip of the sepal
    proper...1. *M. holosericea.*
  Exterior tooth slender, thin, about equaling the free triangular tip of the sepal proper
    2. *M. acuminata.*
  Exterior tooth thickened distally, truncate, about equaling the free subulate tip of
    the sepal proper...................................3. *M. francavillana.*
  Exterior tooth stout, triangular-pyramidal, much exceeding the sepal proper......
    4. *M. gratissima.*
Leaf-blades rounded, clasping, or connate at base, sessile or on petioles rarely more than
  1 cm. long.
  Flowers 6-merous; leaf-blades 7–13-pli-nerved; exterior tooth carinate on the inner
    side.
    Bracts oblong, 5–8 mm. long.
      Exterior tooth salient at nearly a right angle; anthers about 6 mm. long, dorsal
        protuberance none; ovary 4-celled......................5. *M. megaphylla.*
      Exterior tooth erect; anthers about 4 mm. long, with a dorsal protuberance;
        ovary 3-celled...6. *M. ampla.*
    Bracts orbicular, 1 cm. long; exterior tooth erect.............7. *M. involucrata.*
  Flowers 5-merous; leaf-blades 5-pli-nerved, clasping or connate at the sessile base;
    exterior tooth carinate on the outer side....................8. *M. fissa.*

1. MICONIA HOLOSERICEA (L.) Triana. For description and synonymy see Cogniaux, Monogr. Phaner. **7**: 732. Widely distributed from Rio de Janeiro (*fide* Cogniaux) through central Brazil (*Blanchet 603, 1808, Gardner*) to French Guiana (*Le Prieur, Jelski, Poiteau, Melinon, Broadway 728*), British Guiana (*Schomburgk 955/1303, 954/1264, Tate 252*), Trinidad (*Broadway 6455*), the Amazon Valley (*Spruce 1162*), Peru (*Williams 6435, Killip & Smith 24766, 24809*), and Bolivia (*Bang 1647, 1957, Rusby 2250*). It is typically an Amazonian species and the only common and widely distributed member of the group, as the citations above indicate, and the only one well represented in herbaria.

2. MICONIA ACUMINATA (Steud.) Naud. Cogn. *op. cit.* 731. French Guiana (*Martin*) and Surinam (*Hostmann 1265*).

3. MICONIA FRANCAVILLANA Cogn. Cogn. *op. cit.* 733. French Guiana (*fide* Cogn.); tropical Brazil (*Blanchet 3448*). Blanchet's specimen may be regarded as the type. Through the courtesy of the late Dr. Briquet I had opportunity to dissect a flower of the type, confirming beyond doubt the position of the species in this group. Cogniaux' plate indicates a deciduous calyx but fails to show the thickened exterior teeth.

4. MICONIA GRATISSIMA Benth. Cogn. *op. cit.* 732. French Guiana (*Melinon, Wachenheim 99*), British Guiana (*La Cruz 4526*), and the Amazon Valley (*Ule 5971, Spruce 1189*).

5. **Miconia megaphylla** sp. nov. Foliis amplis late ellipticis subsessilibus 9–13-pli-nerviis supra glabris subtus tenuissime tomentulosis; bracteis oblongis deciduis; floribus glomeratis sessilibus 6-meris; hypanthio tubuloso; calyce post anthesin deciduo; sepalis coriaceis ovatis, dentibus exterioribus magnis pyramidatis patulis; staminibus aequalibus, antheris subulatis arcuatis, connectivo simplice; ovario 4-loculare; stigmate truncato.

Stems stout, obscurely and roundly 4-angled, very thinly and closely tomentulose, appearing glabrous, marked by a conspicuous membrane 1–2 mm. wide at each node; petioles stout, pubescent like the stem, 2–3 mm. long; leaf-blades firm, broadly elliptic, as much as 30 cm. long by 19 cm. wide, rounded above to an apiculum 1 cm. long, obscurely crenate, broadly rounded at base, 9–13-pli-nerved, the uppermost laterals arising at about one-fourth the length of the leaf, only the upper two pairs continuous to the summit; upper surface glabrous, the veins conspicuous but nearly plane, the secondaries 6–10 mm. apart, spreading at an angle of 70–90°; lower surface very closely and minutely cinereous-tomentulose, the veins strongly elevated; panicle apparently about 13 cm. long, sparingly branched, its axes rather sharply 4-angled and pubescent with appressed stellate hairs, the nodes and flowers subtended by oblong deciduous bracts 6–8 mm. long; flowers in glomerules of 5–7, 6-merous, sessile; hypanthium tubular, thick-walled, 5.5 mm. long to the torus, thinly gray-tomentulose; calyx deciduous after anthesis, the sepals separate to the torus, thick and coriaceous, increasingly so above, rhombic-ovate, 3.3 mm. long, rather truncate above to a triangular apiculum; exterior teeth very stout and thick, pyramidal, 3-sided, 1.7 mm. long on top, salient at almost right angles, adnate to the sepals to their tips; petals narrowly obovate, 6.5–7 mm. long, rounded above, nearly equilateral, obscurely retuse or entire, glabrous; stamens isomorphic but variable in size; filaments slender, flat, about 6 mm. long; anthers subulate, somewhat arcuate, averaging about 6 mm. long, the pore dorso-terminal; connective simple, split near the base around the insertion of the filament, which therefore appears dorsal, and each half extending back over its theca to the base of the anther; ovary one-third inferior, thick-walled, 4-celled, its glabrous summit conic, obtusely 12-ribbed; style straight, stout, glabrous, 10 mm. long; stigma truncate.

Type, *Buchtien 1108*, collected at San Carlos, in the Mapiri region of Bolivia, alt. 750 m., and deposited in the herbarium of The New York Botanical Garden.

6. MICONIA AMPLA Triana. Cogn. *op. cit.* 729. Endemic to Trinidad (*Lockhart, Broadway 5855, 6144*).

7. MICONIA INVOLUCRATA Donn. Sm. Bot. Gaz. **37**: 209. 1904. Guatemala (*Tuerckheim 8204*) and British Honduras (*Schipp 377*).

8. **Miconia fissa** sp. nov. Caulibus validis glabris; foliis magnis sessilibus amplexicaulibus obovato-oblongis abrupte apiculatis 5-pli-nerviis utrinque glabris; paniculis congestis, floribus fasciculatis, bracteis magnis late rotunda-

tis, 5-meris; hypanthio cylindrico tomentuloso; calyce ad anthesin deciduo, sepalis triangularibus, dentibus exterioribus magnis pyramidatis; petalis obovato-oblongis glabris; antheris subulatis, connectivo ser. ext. supra basin elevato, ser. int. supra insertionem filamenti minute glanduloso; ovario 4-loculare semilibero, stylo elongato.

Apparently a tree or large shrub, with subterete glabrous branches greatly enlarged at the nodes; leaves membranous, oblong-obovate, as much as 22 cm. long by 12 cm. wide, at the tip obtuse or rounded, with an apiculum 10–15 mm. long, entire or obscurely crenate, sessile, certainly clasping, and apparently connate at base, glabrous and shining above, paler green and very minutely pubescent beneath, appearing glabrous, 5-pli-nerved, the uppermost primaries arising 20–25 mm. above the base, the secondaries plane and yellow above, rising at an angle of about 75°, 5–10 mm. apart, the tertiaries obscure above, with the secondaries elevated and reticulate beneath; panicles terminal and from the upper axils, in the former case branched from the base, crowded, 10–15 cm. long, of which the basal half is sterile, their axes rather sharply angled and gray-tomentulose, increasingly so distally; flowers sessile, 5-merous, in small dense clusters subtended by a pair of broadly rotund, tomentulose bracts 10–12 mm. long, composed of a central terminal flower and 2 sessile, lateral, 1–3-flowered clusters each subtended by a pair of similar bracts 8 mm. long and 6 mm. wide, the 1 or 2 lateral flowers of this cluster subtended by bracts 6 mm. long by 3 mm. wide; hypanthium cylindric, 7 mm. long to the torus, 3 mm. in diameter, ribless, closely gray-tomentulose or sericeous; calyx deciduous at or soon after anthesis, its tube prolonged about 0.8 mm.; sepals triangular, 5 mm. long over all, the sepals proper broadly ovate, 3 mm. long, the exterior teeth subterminal, stout, pyramidal, erect, surpassing the sepal proper by 2 mm.; petals obovate-oblong, 8 mm. long, 4 mm. wide, rounded above, glabrous, essentially equilateral, the basal half and a triangular central portion of the distal half fleshy in texture and veinless; stamens slightly dimorphic; filaments stout, flattened, glabrous, the exterior 6.5, the interior 4.8 mm. long; anthers stoutly subulate, nearly straight, 8–8.5 or 7.5 mm. long, opening by a terminal pore, 2-celled, the thecae strongly convoluted, prolonged about 1 mm. and somewhat divergent below the attachment of the filament; connective rounded on the back, near the base in the exterior series prominently elevated into a quadrate protuberance 1 mm. long, the interior series barely elevated into a low protuberance and bearing a conspicuous, sessile, hemispheric gland; ovary about half-inferior, 4-celled, its summit glabrous, narrowed to an erect beak; style 13 mm. long, very thinly and finely pubescent in the basal fourth, tapering to the apex; stigma hemispheric, barely expanded, 0.5 mm. in diameter.

Type, *Holt & Blake 528*, collected on the Rio Maturacá, below Salto de Huá, Amazonas, Brazil, 10–12 Dec. 1930, and deposited in the herbarium of The New York Botanical Garden. *Holt & Blake 468*, collected at the same place three weeks earlier, is the same but immature.

MICONIA SECTION ADENODESMA

Naudin erected the subgenus *Adenodesma* to include three species of *Miconia* with sessile leaves, large flowers, and glandular connectives. His concept was continued by Cogniaux forty years later as a section of the genus, without change in its definition and with the addition of two species which had been unknown to Naudin. Since then three other species have been described.

It is an open question whether a group of species with no more distinctive characters than those mentioned should be given the rank of subgenus or even of section. All three features occur repeatedly elsewhere in the genus, although this is the only group where they occur in conjunction. Careful dissection of the flowers of a majority of the species reveals that two distinct types of stamens are represented and that these types are correlated with equally distinct types of venation and leaf-form. In three species flowers have not been available, but the venation is sufficient to place them in one group or the other and it has been assumed that the stamens would follow the expected pattern if they were known.

The first of these groups contains only two species, *M. macrotis* Cogn. and *M. titanophylla* Gl. The former very closely resembles *M. Boissieriana* Cogn., now placed in the section *Tamonea*, and also suggests by its general habit and structure the common *M. macrophylla* (Don) Triana. These two species are accordingly transferred to *Tamonea*, but as a matter of convenience are still included in the key presented below. The second group includes nine species, all of which properly belong to the section *Adenodesma*. All have large flowers and glandular connectives, but the leaves are not invariably sessile, although always broad and large. In addition to these weak characters the group is distinguished sharply by the shape of the connective, as described more fully in the key below.

Leaves 7–13-nerved, the upper 5–7 primaries traversing the blade and the lower ones entering the conspicuous auricles; flowers often 6-merous. (Stigma, so far as known, capitate; connective, so far as known, prolonged straight back between the bases of the thecae and there obscurely lobed and minutely glandular.) Section TAMONEA, in part.

    Leaves glabrous on the surface above, on the midvein thinly furfuraceous, plane; stem-pubescence of short, delicate, closely matted hairs, stellately branched at the tip, forming a dense indument about 1 mm. thick; flowers 6-merous. . . *M. macrotis*.

    Leaves bullate above, stellate-pubescent on the surface when young, soon becoming glabrate, permanently hirsute on the midvein; stem-pubescence of stout, densely matted hairs, sparsely plumosely branched and stellate toward the tip, forming an indument 4 mm. thick; flowers 5-merous. . . . . *M. titanophylla*.

Leaves 3–5-pli-nerved (sometimes weakly so), usually with an additional pair of obscure marginal veins, the primaries in most species preceded near the base of the

leaf by few to several secondaries; connective (so far as known) widened basally into two lateral deflexed lobes which extend ventrally over the sides of the thecae, are often confluent beneath and always conspicuously glandular, at least along their ventral margins. Section ADENODESMA.

Bracts inconspicuous, setaceous, early deciduous, rarely more than 3 mm. long; calyx open in bud, its lobes regular and obtuse or rounded, or none, the exterior teeth minute or none; stamens isomorphic or nearly so, the lateral lobes of the connective (so far as known) often confluent beneath; stigma not expanded; ovary 3–5-celled.

Stem-pubescence very close and fine, stellate-tomentulose or furfuraceous, forming an indument less than 1 mm. thick and often deciduous on the older parts; peduncle and branches of the inflorescence conspicuously angled.

Lower leaf-surface green, the actual surface plainly visible through the comparatively sparse indument of soft stellate hairs, these mostly limited to the veinlets and with a total spread of 0.2–0.7 mm.; anthers glandular at base of the connective only.

Leaves 3-pli-nerved, exclusive of the marginals; sepals triangular-ovate to semicircular; style and filaments more or less glandular; connective curved at base into a half-circle and bearing numerous glands on each lateral lobe; style 10–15 mm. long.

Leaves thin, obovate in general outline, usually broadest well above the middle, rather shortly acuminate, abruptly contracted below to a broad base which is rounded or cordate to the petiole.........1. *M. amplexans.*

Leaves firm, oblong-elliptic in general outline, broadest near the middle, rather long-acuminate, gradually acuminate below to a narrow base which tapers to the petiole.......................2. *M. tomentosa.*

Leaves 5-pli-nerved, exclusive of the marginals; sepals broadly ovate; style and filaments glabrous; connective lightly curved at base and bearing two stalked glands on each lobe; style 5–6 mm. long........3. *M. biglandulosa.*

Leaves weakly 5-pli-nerved; calyx-limb very thick, the sepals obsolete; style and filaments densely glandular; connective curved into a quarter-circle and densely glandular; style 21 mm. long............4. *M. axinaeoides.*

Lower leaf-surface brown or rufescent, the actual surface completely concealed by the dense indument of sublepidote stellate hairs, covering the surface uniformly and with a total spread of 0.1–0.2 mm.

Leaf-blades dull above, long-acuminate, three times or more as long as broad, rounded or obtuse at base; connective glandular on the back; filaments and style densely glandular............................5. *M. Plukenetii.*

Leaf-blades shining above, acute to obtuse, twice or less as long as broad, distinctly cordate at base (stamens as yet unknown)......6. *M. silicicola.*

Stem-pubescence of stout, spreading, hirsute or plumose bristles 2–5 mm. long.

Leaves strongly bullate above; hypanthium both hirsute and stellate; sepals with a small exterior tooth; ovary 5-celled..................7. *M. rugosa.*

Leaves plane above; hypanthium merely stellate-tomentose; exterior teeth none; ovary 3-celled..................................8. *M. plumosa.*

Bracts conspicuous, oblong or ovate, persistent to anthesis or later, 5–6 mm. long; calyx apparently closed in bud, the exterior teeth adnate, triangular, nearly 2 mm.

long; stamens strongly dimorphic, the lateral lobes of the connective in the smaller
series not confluent beneath; style and filaments densely glandular; stigma capi-
tate; ovary 5-celled....................................9. *M. triangularis.*

1. MICONIA AMPLEXANS (Crueg.) Cogn. For description and synonymy
see Cogniaux, Monogr. Phaner. **7**: 749; Gleason, Bull. Torrey Club **58**: 227.
1931; its geographical distribution is also discussed in the latter article.

2. MICONIA TOMENTOSA (L. C. Rich.) Don. Cogniaux, *op. cit.* 750.
Common and widely distributed throughout the Amazonian region from
Rio de Janeiro (*fide* Cogniaux) and Bolivia (*Williams 567*) to Trinidad;
also in Cuba (*Roig & Van Hermann 1123*) and Isle of Pines (*Jennings 442*);
most abundant in the Guianas. The variety *ovata* Cogn. (*Spruce 814*) is
poorly distinguished by leaf-character only and should not be maintained.
The variety *auriculata* Jennings (*Jennings 442*; type in herb. Carnegie
Museum) is *M. macrophylla* (Don) Triana, as to type specimen and de-
scription; the sheet of the same number in the New York Botanical
Garden is *M. tomentosa.* This species and *M. amplexans* are distinguished
solely by the shape of the leaves and are connected by intergrading forms
with the leaf-base wider than in typical *M. tomentosa* and narrower than in
typical *M. amplexans.* The former is possibly the primitive form, occupy-
ing a rather compact area in northeastern South America, while the latter
occurs chiefly at the margin of this area. I have maintained both species
more for historical reasons than because of actual structural differences.

3. **Miconia biglandulosa** sp. nov. Arbuscula, ramis 4-sulcatis densissime
stellato-furfuraceis; foliis firmulis sessilibus oblongo-obovatis acuminatis
subintegris ad basin subcordatam cuneatis 5-pli-nerviis, supra ad venas fur-
furaceis ceterum glabris, subtus brunneis stellato-pubescentibus; panicula
angustata dense furfuracea; floribus sessilibus 5-meris; hypanthio cylindrico
tomentosulo; calycis lobis ovatis obtusis; petalis oblongo-obovatis; staminibus
subisomorphis; filamentis glabris; antheris subulatis subrectis, connectivo ad
basin curvato dorsaliter paullum elevato, lobis lateralibus ad marginem
glandulis 2 ornatis.

A tree 3–5 m. high, the younger branches conspicuously but roundly
4-angled and 4-sulcate, densely and closely stellate-furfuraceous with bright
brown hairs; leaves firm, sessile, oblong-obovate, 25–35 cm. long, 10–15 cm.
wide, sharply acuminate, subentire, cuneately narrowed from below the
middle to a subcordate base, 5-pli-nerved, with an additional pair of marginal
veins in the basal half only, veins all plane above, elevated beneath, the
secondaries 5–9 mm. apart, ascending at an angle of about 70, the upper
side thinly furfuraceous on the primaries, otherwise glabrous, the lower side
rather densely stellate-pubescent, especially on the veins; panicle narrow, 20
cm. long, densely brown-furfuraceous like the stem, freely branched, the
bracts setaceous, 2 mm. long; flowers sessile, 5-merous; hypanthium cylindric,

5 mm. long to the torus, densely and softly stellate-tomentose; calyx-tube prolonged about 1 mm., the sepals broadly ovate, 0.8 mm. long, very obtuse, pubescent externally like the hypanthium; exterior teeth minute, subterminal; petals narrowly oblong-obovate, 5 mm. long, 2.2 mm. wide, inequilateral, retuse, essentially glabrous; stamens isomorphic but slightly different in size; filaments slender, glabrous, 4 or 5 mm. long; anthers subulate, slightly arcuate, 4 or 5 mm. long, 2-celled; connective slender, elevated near the base into a low dorsal protuberance, the sides of which extend ventrally into 2 lateral lobes over the thecae and bear at the margin of each 2 short-stalked glands; ovary nearly free, subcylindric, 2.8 mm. long, 3-celled, glabrous; style stout, glabrous, 5.6 mm. long, the truncate stigma 0.5 mm. in diameter.

Type, *Killip & Smith 26933*, collected in woods at Iquitos, Peru, alt. about 100 m., and deposited in the herbarium of The New York Botanical Garden. The field notes indicate that the petals are greenish white, the filaments and style white, and the anthers purple.

4. **Miconia axinaeoides** sp. nov. Ramis crassis dense brunneo-tomentosis; petiolis brevibus dense tomentosis; laminis amplis membranaceis late obovatis sursum rotundatis breviter apiculatis integris basi late obtusis sub-5-plinerviis, supra ad venam mediam inferne tomentellis ceterum glabris, subtus ad venas venulasque tenuiter tomentosis ceterum glabris; panicula subsessile pauciflora dense et tenuiter stellato-tomentosa; floribus 5-meris breviter pedicellatis; hypanthio turbinato tenuiter stellato-pulverulento; calycis tubo subampliato truncato, dentibus exterioribus minutis subulatis; petalis obovato-oblongis magnis; staminibus isomorphis; filamentis elongatis complanatis dense glanduloso-pubescentibus; antheris lineari-subulatis thecis convolutis; connectivo basi dilatato in lobos 2 laterales producto ad marginem ventralem stipitato-glandulosos; ovarium inferum 4 (forsan 5)-loculare; stylo elongato glanduloso-pubescente, stigmate parvo.

Upper stems stout and woody, probably considerably flattened, densely brown-tomentose; petioles very stout, 15 mm. long, densely tomentose like the stem; leaf-blades thin and membranous, broadly obovate-oblong, 20–31 cm. long, 13–18 cm. wide, broadly rounded above to a subapiculate tip, entire, broadly obtuse or subrotund at base, weakly 5-pli-nerved, glabrous above except for a little pubescence near the base of the midvein, glabrous beneath on the actual surface, thinly stellate-tomentulose on the veins; secondary veins 6–9 mm. apart, at right angles to the primaries, all veins nearly plane above, lightly elevated and prominently reticulate beneath; panicle nearly sessile, 10 cm. long, its slender axes closely but thinly stellate-tomentose, the lateral branches 2–3-flowered; flowers 5-merous, on pedicels 1–2 mm. long; hypanthium turbinate, 5 mm. long to the torus, very thick and hard, thinly stellate-furfuraceous when young; calyx somewhat spreading, prolonged 2.5 mm. and truncate, the sepals obsolete, the exterior teeth stoutly subulate, 0.6 mm. long, not projecting; petals obovate-oblong, 16 mm. long,

8 mm. wide, nearly equilateral, slightly retuse, glabrous; stamens isomorphic; filaments flat, 14 mm. long, densely glandular-pubescent throughout; anthers linear-subulate, 8.5 mm. long, slightly arcuate, 2-celled, the pollen-sacs strongly convolute; connective somewhat elevated and conspicuously widened at the base, prolonged into two lateral lobes covering the base of the pollen-sacs and stipitate-glandular along the ventral margin; ovary small, inferior, 4- or 5-celled; style somewhat sigmoid and declined, stout, 21 mm. long, densely glandular-pubescent throughout; stigma small, truncate.

Type, *Buchtien 1099*, collected at Sarampiuni, near San Carlos, in the Mapiri region of Bolivia, alt. 600 m., and deposited in the United States National Herbarium, no. 1399445 (duplicate in herb. New York Botanical Garden). Its large flowers and turbinate hypanthium give it an aspect remarkably like an *Axinaea*.

5. MICONIA PLUKENETII Naud. Cogn. *op. cit.* 751. From French Guiana (*Wachenheim*) to British Guiana (*Schomburgk 1008/1727b, Hohenkerk 784, Appun 653, Stockdale 8762, Abraham 105, La Cruz 3600*) and Trinidad (*Crueger, Lockhart, Broadway*).

6. MICONIA SILICICOLA Gl. Bull. Torrey Club **58**: 428. 1931. Mount Roraima (*Tate 212*) and Mount Duida (*Tate 71*).

7. MICONIA RUGOSA Triana. Cogn. *op. cit.* 751. Manáos, Brazil (*Spruce 1718*); apparently known only by the type specimen.

8. MICONIA PLUMOSA Gl. Bull. Torrey Club **52**: 381. 1925. British Guiana (*Gleason 901, Sandwith 272*).

9. **Miconia triangularis** sp. nov. Arbor parva, ramis 4-sulcatis tenuissime stellato-furfuraceis; foliis sessilibus obovatis breviter acuminatis basi rotundatis vel subcordatis 3-pli-nerviis, ad venas utrinque et ad venulas subtus furfuraceis ceterum glabris; panicula angustata, bracteis late oblongis vel obovatis, floribus sessilibus 5-meris; hypanthio campanulato dense stellato; calyce irregulariter fisso hypanthium aequante utrinque pubescente, dentibus exterioribus triangularibus; petalis obovatis inaequilateralibus; staminibus dimorphis connectivo basi glanduloso; ovario 5-loculare.

A tree 3–6 m. high, the younger branches roundly 4-angled and 4-sulcate, thinly but closely stellate-furfuraceous; leaves sessile, firm in texture, obovate to oblong-obovate, as much as 13 by 25 cm., abruptly short-acuminate, minutely and irregularly crenate-denticulate, narrowed from the middle or above it to a rounded or subcordate base, 3-pli-nerved, secondaries arising at an angle of about 80°, 4–8 mm. apart, essentially glabrous above, very thinly furfuraceous on the veins and secondaries beneath; panicle rather narrow, 20–30 cm. long, its branches conspicuously 4-angled and 4-sulcate, tomentulose like the stem; bracts obovate to broadly oblong, 5–6 mm. long, subtending each flower and node, eventually deciduous; flowers sessile, 5-merous; hypanthium campanulate, 3.2 mm. long to the torus, densely and

finely stellate-tomentulose; calyx apparently closed in bud, at anthesis its
tube prolonged 2.5 mm., densely sericeous within, its lobes irregularly tri-
angular, lacerate, 1.6 mm. long; exterior teeth totally adnate, thick and heavy,
triangular, about 2 mm. long; petals elliptic, 9 mm. long, 5 mm. wide, con-
spicuously inequilateral, slightly retuse; filaments densely glandular-pubescent
throughout, 8.5 or 6.5 mm. long; anthers 2-celled, subulate, 7.5 or 5.7 mm.
long; lateral lobes of the connective in the outer series almost confluent be-
neath the anther, densely glandular on the lower half, in the inner series ex-
tending halfway over the side of the anther and bearing a single marginal
row of glands; ovary partly inferior, 5-celled, its free summit very broadly
truncate; style 15 mm. long, densely glandular-pubescent; stigma capitate,
1.5 mm. in diameter.

Type, *Klug 1697*, collected at Umbria on the Putomayo River, Col-
ombia, lat. 0°54′ N., long. 76°10′ W., alt. 325 m., and deposited in the
herbarium of The New York Botanical Garden; *Klug 1790*, from the same
locality, is identical.

PIPTOCARPHA IN ANDEAN SOUTH AMERICA

Piptocarpha R. Br. is a genus of vernonioid composites, distinguished
from *Vernonia* chiefly by the caudate anthers and in a majority of the
species also by the dense axillary inflorescences. The genus is best de-
veloped in southern and eastern Brazil, whence about twenty-five species
are known. A few others occur in the Guianas, Trinidad, and Central
America. Nine species have been accredited to the Andean region, ranging
from Colombia to Bolivia. Of these, *P. elaeagnoides* Baker is best restored
to the genus *Vernonia* as *V. elaeagnoides* HBK., and *P. gracilis* Rusby is
Vernonia gracilis HBK. To the remaining seven there are now to be added
four additional, hitherto undescribed species.

Schultz Bipontinus monographed the genus in 1863, under the name
Carphobolus, basing his six subgenera largely on the character of the in-
florescence. Baker followed essentially the same divisions in his treatment
of the genus for the Flora Brasiliensis in 1873, and the same characters are
again used in the key below, by which eleven Andean species may be
separated.

Inflorescences and individual heads both sessile, axillary; leaves ovate-lanceolate,
    rounded at base, loosely stellate-pubescent beneath; heads with 11 flowers or
    more.
    Heads 11–15-flowered; involucre 10 mm. high....................*P. asterotrichia.*
    Heads about 34-flowered; involucre 15 mm. high....................*P. insignis.*
Inflorescences sessile, axillary, the individual heads distinctly pedicelled, forming a
    sessile umbel; heads about 15-flowered; involucre about 8 mm. high....*P. Lechleri.*
Inflorescences peduncled, axillary, the peduncles few, short, stout, and umbellate, bear-
    ing each a few sessile heads; leaves finely canescent-tomentulose beneath.

Heads about 6-flowered; leaves mostly broadly obtuse or rounded at base........
　　　　　　　　　　　　　　　　　　　　　　　P. Poeppigiana.
Heads about 11-flowered.
　　Flowers 1–3 on each peduncle; leaves of a lanceolate type, broadest below the
　　　　middle, rounded or obtuse at the usually inequilateral base....*P. vismiaefolia.*
　　Flowers 5–10 on each peduncle; leaves of an elliptic type, broadest at the middle
　　　　and acute at both ends.................................*P. longifolia.*
Inflorescence a branched, axillary, corymbiform cluster.
　　Heads 3-flowered...*P. Sprucei.*
　　Heads 5–6-flowered.
　　　　Leaves loosely stellate-pubescent beneath; stems pubescent; branches of the in-
　　　　　　florescence and involucral scales densely gray-tomentose......*P. canescens.*
　　　　Leaves densely and closely canescent beneath with a sublepidote tomentum;
　　　　　　branches of the inflorescence and involucral scales glabrous or nearly so;
　　　　　　stems finely canescent.
　　　　Petioles 15–25 mm. long; inflorescences loosely branched, 2–4 cm. long....
　　　　　　　　　　　　　　　　　　　　　　　P. laxa.
　　　　Petioles about 10 mm. long, about equaling the influorescences.........
　　　　　　　　　　　　　　　　　　　　　　　P. tereticaulis.
Inflorescence a loose, open, freely branched, many-headed, terminal panicle........
　　　　　　　　　　　　　　　　　　　　　　　P. Sodiroi.

Piptocarpha insignis sp. nov. Ramis crassis angulatis primum stellato-
pubescentibus mox glabrescentibus; petiolis brevibus crassis tomentosis;
laminis ovato-ellipticis acutis basi rotundatis supra scabridulis subtus stellato-
pubescentibus venis reticulatis; capitulis sessilibus in axillis inferioribus 5–8
in superioribus paucis vel solitariis, 34-floris; involucri magni obconici squamis
adpressis ovato-lanceolatis pungentibus acuminatis; floribus cum paleis
linearibus immixtis; achaeniis glabris; pappo albido uniseriato.

　　A shrub 1.5–2 m. high, the upper branches stout, strongly angled, densely
but evanescently stellate-pubescent, the internodes 3–5 cm. long or much
shorter at the summit of the stem; petioles stout, 8 mm. long, densely stel-
late-tomentose; leaf-blades ovate-elliptic to ovate-oblong, firm, opaque, about
15 cm. long by 6.5 cm. wide, acute, entire, rounded at the inequilateral base,
the upper side thinly pubescent on the midvein, minutely scabrellate on the
surface, the secondary veins slightly impressed, the veinlets obscure, the
lower side stellate-pubescent with stalked hairs bearing 3 or 4 terminal
branches, thinly so on the surface, densely on the midvein, the veins and
veinlets elevated and conspicuously reticulate; inflorescences axillary, forming
clusters of 5–8 sessile heads in the lower axils, reduced to few or solitary heads
and approximate at the summit of the branch; heads about 34-flowered; in-
volucre obconic when pressed, 15 mm. long, its scales appressed, ovate-
lanceolate, pungently acuminate, glabrous; flowers subtended by linear
acuminate scales 12 mm. long; achenes glabrous, angulate, 4 mm. long; pappus
nearly white, 7 mm. long, an outer series not differentiated.

Type, *Killip & Smith 26083*, collected in dense forest at San Nicolas, Pichis Trail, Dept. Junín, Peru, alt. about 1100 m., and deposited in the herbarium of The New York Botanical Garden.

Piptocarpha vismiaefolia sp. nov. Ramis gracilibus subteretibus tenuiter canescentibus; petiolis elongatis canescentibus; laminis lanceolatis mediocris acuminatis basi obtusis, supra praeter venam mediam pubescentem glabris subnitentibus, subtus canescenti-tomentosulis venis elevatis reticulatis; pedunculis paucis crassis brevibus axillaribus, capitulis in quoque pedunculo 1–3 sessilibus terminalibus parvis 6-floris; floribus achaeniis et pappo ignotis.

A shrub 3–4 m. tall, the upper branches slender, slightly angled, thinly cinereous-tomentulose, the internodes 3–4 cm. long; petioles rather stout, 15–20 mm. long, densely cinereous-tomentulose; leaf-blades firm, lanceolate, as much as 16 cm. long by 5.5 cm. wide, long-acuminate, entire, rounded or obtuse at the usually inequilateral base, the upper side minutely pubescent on the midvein, glabrous and somewhat shining on the surface, the veins and veinlets nearly plane and very finely reticulate, the lower side densely cinereous-tomentulose with sublepidote hairs, the veins and veinlets prominently elevated and reticulate; inflorescence axillary; peduncles several (about 5), stout, 3–5 mm. long, densely brown-tomentulose, each bearing 1–3 sessile terminal 11-flowered heads; involucre subglobose when young, becoming campanulate in age, 4–5 mm. long, its scales broadly ovate, obtuse, thinly pubescent when young, glabrous at maturity; flowers, achenes, and pappus immature in the type.

Type, *Killip & Smith 23848*, collected in dense forest east of Quimirí Bridge, near La Merced, Dept. Junín, Peru, alt. 800–1300 m., bearing immature flowers in June, and deposited in the herbarium of The New York Botanical Garden; *Williams 6675*, from Alto Río Huallaga, Dept. San Martín, alt. 360–900 m., with mature empty involucres in December, is the same.

Piptocarpha longifolia sp. nov. Ramis gracilibus subangulatis tenuiter canescentibus; petiolis angulatis elongatis dense tomentosulis; foliis anguste ellipticis acuminatis basi acutis supra glabris venis planis, subtus canescenti-tomentosulis venis elevatis reticulatis; pedunculis paucis crassis brevibus axillaribus; capitulis 13-floris in quoque pedunculo 5–10 sessilibus vel breviter pedicellatis; involucri ovoidei squamis late ovatis obtusis parce ciliatis; floribus cum paleis immixtis.

A slender tree 3–4 m. tall, the upper branches apparently elongate, slender, conspicuously angled, very thinly cinereous-tomentulose, the internodes 3–5 cm. long; petioles slender, strongly angled, 15–20 mm. long, densely cinereous-tomentulose; leaf-blades firm, narrowly elliptic or elliptic-oblong, as much as 21 cm. long by 6 cm. wide, broadest at the middle, sharply but abruptly acuminate, entire, acute at the base, glabrous above with plane veins and finely and inconspicuously reticulate veinlets, densely gray-tomen-

tulose beneath, the veins and veinlets strongly elevated and prominently reticulate; inflorescences axillary, each flowering node bearing several (3–6), stout, somewhat flattened, densely tomentulose peduncles 5–10 mm. long; heads 5–10 on each peduncle, sessile or on pedicels as much as 2 mm. long, 13-flowered; immature involucres ovoid, 4–5 mm. long, the scales appressed, broadly ovate, obtuse, often minutely ciliate; flowers (now immature) mingled with subtending scales.

Type, *Killip & Smith 25459*, collected in dense forest at Yapas, Pichis Trail, Dept. Junín, Peru, alt. 1350–1600 m., and deposited in the herbarium of The New York Botanical Garden.

Piptocarpha canescens sp. nov. Foliis magnis ovato-lanceolatis basi rotundatis supra opacis reticulatis subtus dense stellato-pubescentibus venis elevatis et arcte reticulatis; cymis axillaribus globosis multifloris congestis ramosis pedunculo brevioribus, ramis tomentosis gracilibus; involucri ovoidei 6-flori squamis adpressis ovatis acutis ad apicem tomentosis.

A tree 3–4 m. high, the upper branches slender, apparently elongate, nearly terete, densely pubescent with grayish hairs, the internodes about 5 cm. long; petioles stout, 1–2 cm. long, densely tomentose; leaf-blades thin, ovate-oblong to elliptic-oblong, as much as 21 cm. long by 10 cm. wide, broadest at or below the middle, subacuminate, entire, broadly rounded at base, the upper side densely stellate-pubescent on the midvein, essentially glabrous on the opaque surface but probably thinly stellate-pubescent when young, the lower side rather softly pubescent with stalked stellate hairs bearing 3–5 spreading terminal branches; primary and secondary veins impressed above, elevated beneath, the veinlets elevated and finely reticulate on both sides; inflorescences axillary, about 2 cm. in diameter when pressed, freely branched, each with about 40 heads, the branches slender, densely stellate-tomentose; pedicels about 1 mm. long; immature involucres campanulate or ovoid, 3–4 mm. high, the scales ovate, acute, densely tomentose on the exposed tips; flowers 6, the corollas, achenes, and pappus immature in the type.

Type, *Killip & Smith 26084*, collected in dense forest at San Nicolas, Pichis Trail, Dept. Junín, Peru, alt. about 1100 m., and deposited in the herbarium of The New York Botanical Garden.

The recent collections by Killip & Smith also include the following species:

PIPTOCARPHA ASTEROTRICHIA (P. & E.) Baker. San Ramón, Dept. Junín. 900–1300 m., *24747*.

PIPTOCARPHA OPACA (Benth.) Baker. Manáos, Brazil, *30111*.

PIPTOCARPHA POEPPIGIANA (DC.) Baker. Lower Río Huallaga below Yurimaguas, Dept. Loreto, *28803*; Iquitos, Dept. Loreto, *26913*; along Río Marañon, near mouth of Río Tigre, *27527, 27529*. The last specimen cited has conspicuously broader leaves, truncately rounded at the base.

TWO PERUVIAN SPECIES OF VERNONIA

Vernonia Fieldiana sp. nov. *Scorpioideae Foliatae,* caule subtcrete tenuiter tomentoso; foliis firmulis subsessilibus ovato-oblongis subacuminatis integris basi rotundatis, utrinque dense sed inconspicue pubescentibus, venis lateralibus curvato-adscendentibus subtus prominentibus; inflorescentia congesta multiflora, bracteis minutis; capitulis sessilibus 11-floris; involucri squamis laxe imbricatis acutis non carinatis subtomentosis ex infimis triangularibus ad interiores ovato-lanceolatas variantibus; corollae tubo lobos subaequante; achaeniis dense sericeis; pappi paleis lanceolato-oblongis quam setis interioribus albis 4–5-plo brevioribus.

Upper stems slender, nearly terete, densely and closely cinereous-tomentose, the internodes about 1 cm. long; petioles stout, 1 mm. long; leaf-blades firm, dull green, ovate-oblong, as much as 35 mm. long by 19 mm. wide, sharply acute or subacuminate, entire, rounded at base, both sides closely but inconspicuously pubescent with minute slender hairs, lateral veins curved-ascending and parallel, strongly elevated beneath; inflorescence a crowded, many-flowered, compound, scorpioid cyme, its short axes densely and softly cinereous-tomentose; bracts seldom more than 5 mm. long; involucre campanulate when dry, 5 mm. high, its scales loosely imbricate, sharply acute, not carinate, densely subtomentose, the outermost triangular, the inner ovate-lanceolate and as much as 3.4 mm. long; flowers 11 in each head; corolla 5 mm. long, the tube about equaling the lobes, glabrous; anthers 2.2 mm. long; style-branches 1.5 mm. long; achenes densely sericeous; paleae lanceolate-oblong, 0.8 mm. long; bristles white, 3.5 mm. long.

Type, *Williams 7663*, collected at San Roque, Dept. San Martín, Peru, alt. 1350–1500 m., and deposited in the National Herbarium as no. 1495545. *V. Fieldiana* closely resembles *V. Mandonii* Sch.-Bip. in foliage and general habit, but in the latter species the leaves are much more densely pubescent, the bracts are larger, the pappus is tawny, and the outer scales of the involucre are linear-subulate and subspinose at tip.

Vernonia albifila sp. nov. *Lepidaploa,* fruticosa erecta caule obscure angulato pubescente; foliis elliptico-oblongis acuminatis ad basin in petiolum brevem cuneatis minute denticulatis supra tenuiter papilloso-pubescentibus subtus minutissime albo-pubescentibus; panicula ampla ramosa pubescente; capitulis sessilibus sub-18-floris; involucri squamis adpressis brevibus subacutis arachnoideo-pubescentibus; corolla glabra; achaeniis obscure angulatis pubescentibus; pappi paleis linearibus, setis ca. 35 albidis.

Erect shrub 3 m. high, the upper branches slender, obscurely but rather sharply angled, thinly but closely pubescent, the internodes 2–3 cm. long; leaf-blades thin, elliptic-oblong, 7–9 cm. long, 2–3 cm. wide, sharply acuminate, cuneate at base into a petiole 3 mm. long, very minutely and remotely denticulate, lustrous and minutely papillose-pubescent above, minutely

pubescent with white hairs beneath; inflorescence a corymbiform panicle, freely branched, 15 cm. long and wide, leafless except at base of the lower branches, its axes softly pubescent; heads very numerous, sessile, about 18-flowered; involucre subglobose, campanulate when pressed, about 5 mm. high, its scales spirally imbricate, appressed, bluntly acute, arachnoid-pubescent, thin at the margins, dark-colored on the exposed tips, never carinate, ranging from ovate-triangular and 1.3 mm. long through ovate, 1.6 mm. long, to elliptic-oblong, 3.2 mm. long, and linear-oblong, 3.7 mm. long; corolla-tube 4.4 mm. long, gradually expanded distally, the lobes oblong-lanceolate, acute, 2.2 mm. long; anthers 2.8 mm. long, with lanceolate appendages 0.7 mm. long; styles minutely pubescent externally, their lobes 3.4 mm. long; achenes obscurely angled, 1.6 mm. long, thinly pilose; pappus-paleae linear-lanceolate, 0.4–0.6 mm. long; bristles about 35, nearly white, 5.6 mm. long.

Type, *Killip & Smith 30102*, from sandy woods at Manáos, State of Amazonas, Brazil, alt. 25 m., deposited in the herbarium of The New York Botanical Garden. The species is related to *V. polyanthes* (Spreng.) Less., which has longer and narrower, more densely pubescent leaves, thinner, blunter, and smoother involucral scales, and tawny pappus.

A NEW BLAKEA FROM COLOMBIA

Blakea bracteata sp. nov. Frutex scandens, ramis, petiolis, laminis, pedunculis et bracteis utrinque hirsutis; foliorum laminae oblongo-ellipticae breviter et anguste acuminatae, basi acutae 3-nerviae; pedunculi graciles axillares solitarii; bracteae externae late deltoideo-ovatae breviter acuminatae basi truncatae, internae oblongae acutae; hypanthium hemisphaericum glabrum; calyci limbus patens glaber, lobi triangulari-oblongi acuti hirsuti; petala obovata acuminata; filamenta antheras subaequantia; antherae in annulo conniventes crassae semi-ovoideae, poris 2 minutis terminalibus dehiscentes, connectivo crasso infra insertione filamenti brevissime producto et truncato.

A climbing shrub, the slender branches, petioles, leaf-blades, peduncles, and bracts hirsute throughout with purple-brown hairs 2–4 mm. long; leaves apparently equal and unequal in alternate pairs, the slender petioles 10–25 mm. long; blades thin, elliptic-oblong, as much as 13 cm. long by 5.5 cm. wide, abruptly short-acuminate, entire, acute or rarely obtuse at base, 3-nerved; veins not prominent, barely elevated beneath, the secondaries 3–5 mm. apart, ascending at an angle of 70°; peduncles solitary in the upper axils, 1–3 cm. long, slender; bracts separate to the base, the outer deltoid-ovate, 15 mm. long, 16 mm. wide, abruptly short-acuminate, broadly truncate at base, the inner oblong, 12 mm. long, 5 mm. wide, subacute, the basal third or half glabrous, the distal portion hirsute; flowers 6-merous; hypanthium hemispheric, glabrous, about 9 mm. in diameter; calyx membranous or nearly scarious, its glabrous tube spreading, 1.4 mm. wide, with broadly rounded sinuses; sepals triangular-oblong, thin, 4.5 mm. long, acute or subacute, densely hirsute on

both sides and margins; petals obovate, 13 mm. long, 8.5 mm. wide, acuminate glabrous except for 1 or 2 short bristles at the apex; filaments stout, flat, glabrous, 4 mm. long; anthers coherent in a ring, stoutly semi-ovoid, 4 mm. long, each theca opening separately by a minute terminal pore; connective very thick, barely prolonged below the filament into a fleshy truncate dorsal appendage; ovary wholly inferior, its top concave from sides to middle, where it is elevated into a short subcylindric beak; style straight, glabrous 8 mm. long; stigma subcapitate.

Type, *Klug 1669*, collected at Umbria, Comisaría del Putumayo, Colombia, at. 0° 54′ N., long. 76° 10′ W., alt. 325 m., in forest, and deposited in the herbarium of The New York Botanical Garden; *Klug 1824*, from the same locality, is identical.

The distant secondary veins give *B. bracteata* an aspect quite unlike other species of the genus. Hirsute pubescence and thin leaves are also the exception in *Blakea*. Our plant is apparently most nearly related to *B. hirsuta* Berg, in which the leaves are much larger and nearly smooth, the flowers subsessile, and the calyx glabrous.

THE NEW YORK BOTANICAL GARDEN

INDEX TO AMERICAN BOTANICAL LITERATURE
1930–1932

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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The development of the embryo of Kochia scoparia

MARION E. WILLIAMS

(WITH PLATES 25 AND 26)

INTRODUCTION

The study of the development of the embryo of *Kochia scoparia* (L.) Roth was suggested because of the transparent seed coats in this species. The embryo, lying in a watery embryo-sac, may be distinctly seen in a seed which is under the dissecting microscope. For this reason, selection of embryos in successive stages of development is easily made; moreover, since the flowers appear as the stem elongates, mature seeds may be found on the same branch that bears unfertilized ovules.

Few of the Chenopodiaceae have been studied from the point of view of the development of the embryo. Comprehensive works on the embryo-sac by Dahlgren (1916) and Fischer (1880), on endosperm by Hegelmaier (1885), and on seed coats by Netolitzky (1926) include investigations on members of this family. Other studies dealing specifically with the Chenopodiaceae also emphasize these phases of seed study, only briefly describing the embryo. Extensive work has been done, however, by Souèges (1920) on the embryo of *Chenopodium bonus-henricus*. It is with this species, therefore, that *Kochia scoparia* is compared in this paper, with occasional reference to descriptions reported for other related genera and families.

MATERIALS AND METHOD

Material was collected throughout the summer and fall from both the cultivated plants and escapes. Ovules were removed under a binocular dissecting microscope and placed immediately into formalin acetic-alcohol.[1] Best results in fixation were obtained when the cells were completely water-filled. When collections were made in the afternoon, the flower-bearing branches were submerged in water for ten minutes and then placed in a moist chamber until the leaves were markedly turgid. After this treatment the embryo-sacs were less plasmolyzed and were more suitable for fixation. Some of the larger embryos were removed from the ovules before immersion in the fixing solution. Entire flowers and fruits were also preserved, although penetration through the many layers was too slow to give good results in fixation.

[1] Formula: 100 cc 50% alcohol
    10 cc neutral formalin
    7 cc glacial acetic acid

In preparation for imbedding in paraffin, the smaller ovules were lightly stained so that their position in the paraffin block might be more easily determined.

Old ovules and embryos were cut 5–8μ thick; young ovules and flowers, 8–12μ. Sectioning at any stage was extremely difficult. Young ovules tend to be spherical so that sections, intended as longitudinal cuts of the embryo sac, often proved to be transverse or oblique. Orientation of the older flattened ovules was less difficult, but due to the starch which filled the cells of the perisperm they did not section readily. This was remedied by trimming the paraffin block closely and placing it in water for a time, varying from one to three weeks.

THE OVULE

The ovule is that typical of the Chenopodiaceae and all other families of Engler's order Centrospermae. It is campylotropous, arising at the base of the ovary on a short funiculus that becomes longer and more slender as the ovule bends over it. Both the micropylar and chalazal ends of the ovule bend down toward the base of the funiculus which at the same time is pushing upward into the concavity. Finally the ends of the ovule come close together, often slightly overlapping, and within, the perfectly horseshoe-shaped embryo-sac encircles a region of perisperm.

In the young ovule (fig. 19), the two integuments are each composed of two layers, each layer one-cell thick. At the micropyle, the cells of the inner integument are much enlarged and extend beyond the margins of the outer integument. As the ovule develops, the integuments are stretched and digested until the identity of the cells may be entirely lost. A homogenous layer (fig. 20, d) is laid down between the nucellus and the inner integument, appearing before the formation of the embryo and becoming more pronounced as the ovule matures. By the Sudan III test, the presence of suberin in this layer was indicated. In sections, this layer was deeply stained by gentian-violet. The perianth parts, with the ovary wall, are retained about the seed at maturity.

THE EMBRYO-SAC

The embryo-sac is early buried deep in the nucellus, situated, as Hegelmaier (1885) describes, closer to the chalazal end of the ovule than to the micropylar end (fig. 19). A similar condition in *Chenopodium foetidum* is explained by Fischer (1880) as being due to the rapid division of a line of cells formed from the original tapetal cell. The arrangement of the cells in parallel rows in the micropylar region of the nucellus indicates that this same progression of cells may take place in *Kochia scoparia*.

The embryo-sac is of the normal eight-nucleate type as has been reported in *Chenopodium foetidum* by Fischer (1880), in *Atriplex hortensis* by Cohn (1914), in *Hablitzia tamnoides* by Dahlgren (1916), in *Salsola Kali* by Romell (1919), and in *Beta vulgaris* by Artschwager (1927). The antipodals disappear quickly and were observed in *Kochia scoparia* only in a disintegrated form. In this condition they were not easily distinguished from the adjacent cells of the nucellus which were being absorbed by the enlarging embryo-sac. The synergids, too, are short lived. They were however, identified in many sections, being long and narrow in outline and lying close to the egg. The polar nuclei fuse before fertilization. The nucleus thus formed is large with a brightly staining nucleolus and lies near, or in contact with, the egg nucleus. Apparently the embryo-sac remains in this stage for a long period, since most of the sections showed this two-nucleate condition. An identical embryo-sac is described by Gibbs (1907) for *Stellaria media* of the Caryophyllaceae. Early fusion of the polar nuclei is also described in *Chenopodium foetidum* by Fischer (1880).

The embryo-sac enlarges by digestion of the surrounding nucellar tissue even before the complete eight-nucleate condition is attained. After the formation of the endosperm nuclei the sac rapidly elongates, keeping far in advance of the embryo. The nucellus is finally absorbed almost to the chalazal end of the ovule, with but one or two nucellar layers remaining between the sac and the integuments.

THE ENDOSPERM

Division of the endosperm nucleus takes place before that of the fertilized egg. The resulting endosperm is free-nuclear as is reported by Hegelmaier (1885), forming a deeply staining cap over the suspensor (fig. 20), and later, the lower half of the embryo. By the time the cotyledons appear, wall formation has taken place in this micropylar region, the endosperm cells becoming conspicuously vacuolated. Sections did not verify Hegelmaier's statement that the endosperm reaches only two-thirds of the distance to the chalazal end of the sac. On the contrary, a second endosperm cap is formed at the chalazal end, remaining free-nuclear and digesting the tissue ahead of it (fig. 20). The elongation of the embryo-sac is brought about by the action of this portion of the endosperm.

Between the two caps the endosperm is at first but a peripheral layer of cytoplasm with a few scattered nuclei. As the embryo elongates, the cellular micropylar cap advances into this mid-region and slightly fills in the space between the cotyledons when the embryo is at the stage illustrated in figure 32. A peripheral layer of endosperm, one-cell thick, lines the remainder of the embryo-sac until it merges into the free-nuclear en-

dosperm which occupies the chalazal end. Thus the embryo is completely enclosed in a loose sac of endosperm which often remains about it when the embryo is lifted out from the ovule.

THE PROEMBRYO

The proembryo like that of *Chenopodium bonus-henricus* is markedly filamentous (figs. 1–10), a characteristic due to the number of transverse divisions that take place before the first vertical wall appears. The stage at which this vertical division is made varies but it usually occurs at or soon after the six-celled stage. Even then, contrasting with *Capsella* whose embryo was for a long time considered typical of dicotyledons, the vertical division of the apical cell is delayed until after such divisions have occurred in the cells in the several tiers below. Figure 8 shows an embryo in which longitudinal division has taken place in the fifth and seventh tiers but not in the upper four.

Figure 7 shows one in which the cells of the first and second tiers have divided vertically; in that shown in figure 9, a vertical wall occurs in the third tier also. The comparative development of the cells indicates that the apical cells have divided recently. In no case was a vertical wall seen in an apical cell only. In the embryo illustrated in figure 10, the upper three tiers have reached the same stage of development, having divided once in the plane parallel to the page and one of each pair of daughter cells having redivided in a plane at right angles to that of the previous division.

As in *Chenopodium bonus-henricus*, when the embryo proper becomes differentiated, the suspensor is seen to develop from two tiers which, in dividing, become four, the uppermost being the hypophysis (figs. 9, 10). The embryo proper develops from four tiers which are easily distinguished as the change from the linear to the spherical form takes place (figs. 9–12; 14–18). Souèges, however, describes the embryo of *Chenopodium bonus-henricus* as including but three tiers. This situation occurs as an occasional exception in *Kochia scoparia* as is shown in figure 13.

THE SUSPENSOR

The suspensor remains characteristically linear. The identity of the three cells below the hypophysis is soon lost by their multiplication into a long row of cells which vary in size and in number (figs. 11–17). Only rarely were the suspensor cells seen to have divided vertically. Two such exceptions are shown in figures 8 and 13. Maturing embryos, removed from the ovules, still retained a portion of the filamentous suspensor (figs. 29–34). In sections of the ovule, even in advanced stages, the row of cells was seen buried in the endosperm cap at the micropylar end. Only in the

mature seed when the endosperm had been obliterated was the suspensor lacking (fig. 35).

The basal cell of the suspensor is greatly enlarged and vacuolated in the early stages. It is buried in the nucellar tissue, as shown in figure 20, behind the endosperm cap which surrounds the rest of the suspensor. In later stages (figs. 11–17), it becomes irregular in shape and size as the nucellar tissue about it is digested by the endosperm. At the same time, adjacent cells of the suspensor may also become distorted.

It is in the structure of the suspensor that the only striking difference appears in the embryos of *Kochia scoparia* and *Chenopodium bonus-henricus*. Souèges' illustrations show the filamentous suspensor only up to the time the embryo is about four cells in diameter. At this stage, vertical divisions occur, followed by many irregular divisions which result in a massive, club-shaped suspensor.

THE HYPOPHYSIS

The hypophysis is differentiated in the linear embryo, occupying the fifth layer in an embryo of eight tiers (figs. 9, 10). Division of the hypophysis takes place about the time the embryo begins to take on its spherical form. The first walls are usually two vertical ones at right angles to each other so that a plate of four cells results. Exceptions, however, are shown in figures 11 and 20, where a horizontal wall was first formed. Horizontal division of the four-celled plate caused two layers to be formed, the upper layer extending laterally to complete the dermatogen, the lower layer forming the root-cap initials (figs. 20–22, 24). This corresponds to the behavior of the hypophysis of *Chenopodium bonus-henricus*.

Figure 17 illustrates a condition often seen in sections cut several cells thick. The upper part of the hypophysis bulges into the center of the embryo and seems to push the innermost cells upward as it does in *Capsella*.

THE DIFFERENTIATION OF THE HISTOGENS

The dermatogen is cut off early, usually when the third tier of the embryo consists of a quadrant of cells. A periclinal wall segments each of the four cells, and as the embryo enlarges, walls are formed in a similar position in the tiers above and below (figs. 11–14). The dermatogen is then complete except for that of the root tip which is to be formed later by the hypophysis as has been described.

The periblem is first distinquished when the embryo attains a diameter of five or six cells (figs. 12–14), as the row of cells just within the dermatogen. The remaining cells in the one or two rows at the center are those from which the plerome will be developed. As in *Chenopodium bonus-henricus*, the lowest tier of the embryo proper contributes the plerome and

periblem initials in the root. This situation is illustrated in figure 18. (The demarcation between the four tiers in the embryo is emphasized by heavier lines.) In older embryos (figs. 22, 24) distinction between the plerome and periblem is more easily made.

The formation of the histogens in *Kochia scoparia* as in *Chenopodium bonus-henricus* presents a variation from the *Capsella* type in which the periblem initials of the root tip originate from the uppermost half of the hypophysis.

LATER STAGES OF THE EMBRYO

The drawings in figures 28–35 illustrate the general outline of the embryo after the formation of the cotyledons. The bending of the embryo begins early (fig. 30) and continues until the tip of the innermost cotyledon meets the end of the root (fig. 35). The outer cotyledon does not increase in length to reach the end of the embryo-sac as it does in the similar horseshoe-shaped embryo of *Mirabilis jalapa* described by Woodcock (1928). It appears even shorter than the inner cotyledon because of its position on the periphery. In the mature embryo the length of the cotyledons is only slightly less than that of the hypocotyl and radicle.

Figure 22 shows an embryo when the cotyledons are well differentiated. All of the cells are large and tend to be isodiametric except for the procambium. The procambial strand forks at the apex, passing into the cotyledons for a short distance. At this stage no connection is made between the central strand and the plumule.

At the stage pictured in figure 32, the outline of the central strand is sharply marked (fig. 24), and the procambium extends about three-fourths of the distance to the tips of the cotyledons. No differentiation in size or shape of other cells in the cotyledon is seen at this stage (fig. 23).

Figures 25, 26, and 27 are sections from the mature embryo shown in figure 35. The median longitudinal section of the cotyledon (fig. 25), when compared with that in the figure above, shows a marked difference in cellular structure. Two or three rows of palisade parenchyma are indicated on the inner side of the cotyledon, which corresponds to the upper side when the cotyledon is expanded. A massive procambium running out to the tip of the cotyledon separates the palisade from large irregularly-placed cells on the opposite side of the cotyledon. Sections other than median ones show that the procambial strand is branched, indicating the course of the lateral veins in the leaf.

In figure 26 is shown a cross section of the procambial strand just below the point of forking. Figure 27 illustrates the forking of the central strand where the procambium passes into the cotyledons. The procambium is seen

to branch from the cotyledonary strand and enter the plumule. Although the formation of tracheary tubes does not occur in the embryo of the mature seed, the path of the procambium indicates that at the cotyledonary node the change from the protostele, typical of the root, to the siphonostele of the stem takes place.

<div align="center">DISCUSSION</div>

Five types of dicotyledonous embryos are described by Schnarf (1928). The first is the Cruciferan, in which the apical cell of the two-celled embryo first divides vertically and in which the basal cell contributes only the suspensor and the hypophysis of the embryo. In the Asteracean type the apical cell also divides vertically, but the basal cell adds to the lower part of the embryo proper as well as forming the suspensor and hypophysis. The Solanacean, the Chenopodiacean, and the Caryophyllacean types are characterized by transverse division of the apical cell. In the first, however, the basal cell forms only the suspensor and hypophysis; in the second, it contributes the lower half of the embryo as well; and in the last, the basal cell does not divide at all but remains one-celled.

The embryo of *Chenopodium bonus-henricus*, as Souèges' drawings illustrate, represents the Chenopodiacean type. The resemblance of the embryo of *Kochia scoparia* to that of *Chenopodium bonus-henricus* indicates that its development also follows the Chenopodiacean pattern. Mitotic figures, however, were not observed in the critical stages, consequently the part played by each of the initial cells cannot be positively determined.

<div align="center">SUMMARY</div>

1. The ovule of *Kochia scoparia* is campylotropous; at maturity the horseshoe-shaped embryo-sac surrounds a region of perisperm. There are two transparent integuments, the inner one protruding beyond the outer one at the micropyle.

2. The embryo-sac is early buried deep in the nucellus. It is eight-nucleate, although it is often seen with but two nuclei, the endosperm nucleus and the egg. This is due to the early disappearance of the antipodals and synergids, and the fusion of the polar nuclei.

3. The proembryo is characteristically linear, the vertical division of the apical cell being long delayed.

4. The spherical embryo is composed of four tiers, the upper two contributing to the plumule and cotyledons. The third, where the dermatogen is first cut off, contributes the hypocotyledonary region; the fourth, the plerome and periblem initials.

5. The hypophysis divides first vertically then horizontally. Two plates of cells are formed, the upper one of which by lateral extension of cells

completes the dermatogen, the lower one furnishes the root-cap initials.

6. The suspensor, at first two-celled, divides into four, the uppermost being the hypophysis. Transverse divisions take place rapidly, so that the suspensor becomes a long filament.

7. The endosperm is at first free-nuclear, forming two caps at the ends of the embryo-sac. Later, cells appear in the micropylar region which extend to the middle of the sac and form a loose covering over the embryo. The cap at the chalazal end remains free-nuclear and is finally obliterated by the growth of the embryo.

8. The embryo curves until in the mature seeds the tip of the innermost cotyledon meets the radicle.

9. In the mature embryo the solid procambial strand forks at the cotyledonary node and passes out to the tips of the cotyledons. As the procambium enters the cotyledon, a branch turns off which supplies the plumule.

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Description of plates

(All figures drawn by means of the camera-lucida)

PLATE 25

Figs. 1–18. Series showing development of embryo through spherical stage; *h*, the hypophysis; heavier lines mark boundaries of the four tiers of the embryo. (All ×450.)

Fig. 19. Diagrammatic sketch of longitudinal section of young ovule; *a*, outer integument; *b*, inner integument; *c*, nucellus; lines and dots represent arrangement of cells of nucellus. (×65).

Fig. 20. Longitudinal section through embryo-sac of older ovule; endosperm caps shown, also disintegrating nucellar cells; *a*, outer integument reduced to one row of cells; *b*, inner integument represented as dark line, identity of cells having been lost; *c*, homogeneous suberized layer, represented as clear space; *d*, outer row of cells of nucellus. (×65).

PLATE 26

Fig. 21. Embryo with cotyledonary lobes and plumule forming; original outline of hypophysis indicated; plerome, periblem, and dermatogen distinctly marked. (×300).

Fig. 22. Stage with cotyledons well developed, procambium passing into them a short distance. Heavy lines emphasize regions of root tip. (×300).

Fig. 23. Median longitudinal section of cotyledon of the embryo shown in fig. 32. (×217).

Fig. 24. Longitudinal section of radicle tip of same embryo, root cap initials shown. (×300).

Fig. 25. Median longitudinal section of cotyledon of mature embryo in fig. 35, showing differentiation of tissues. (×217).

Fig. 26. Cross section of central strand of mature embryo just below the point of forking. (×217).

Fig. 27. Median longitudinal section of mature embryo at cotyledonary node; procambium forks and passes out into the cotyledons; branch of cotyledonary procambium supplies the plumule. (×217).

Figs. 28–35. Series of outline drawings of embryo from appearance of cotyledons until maturity. (All ×20).
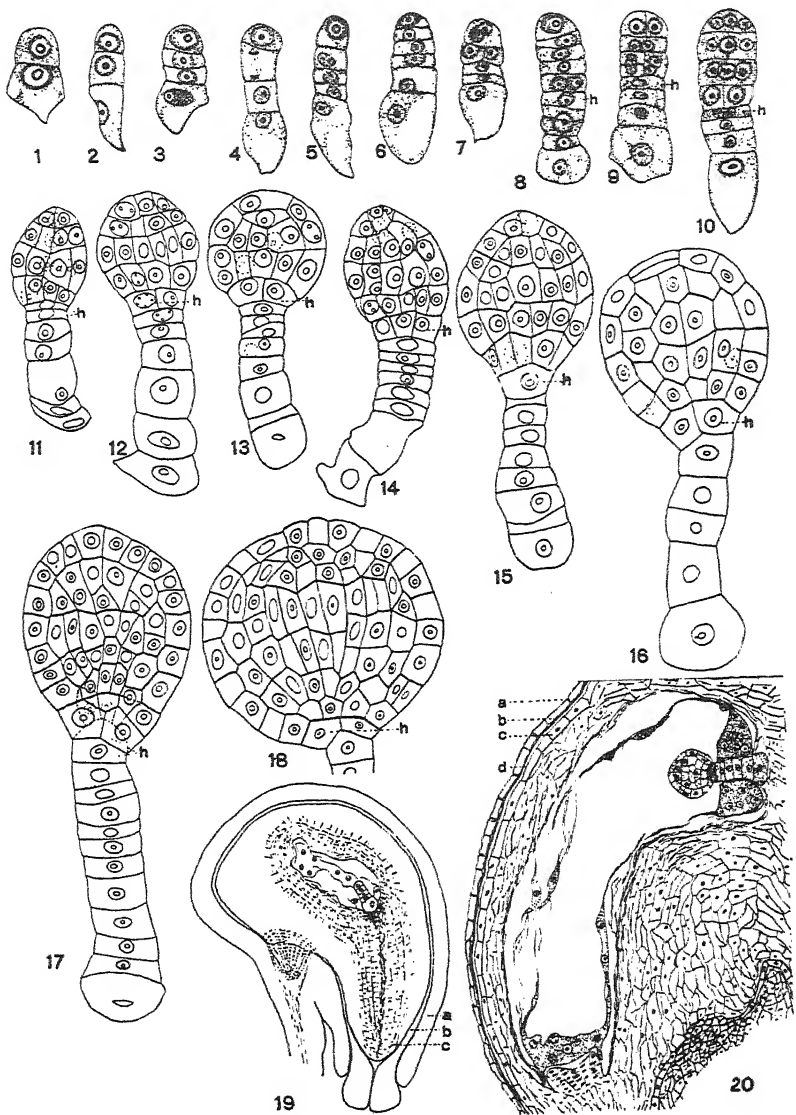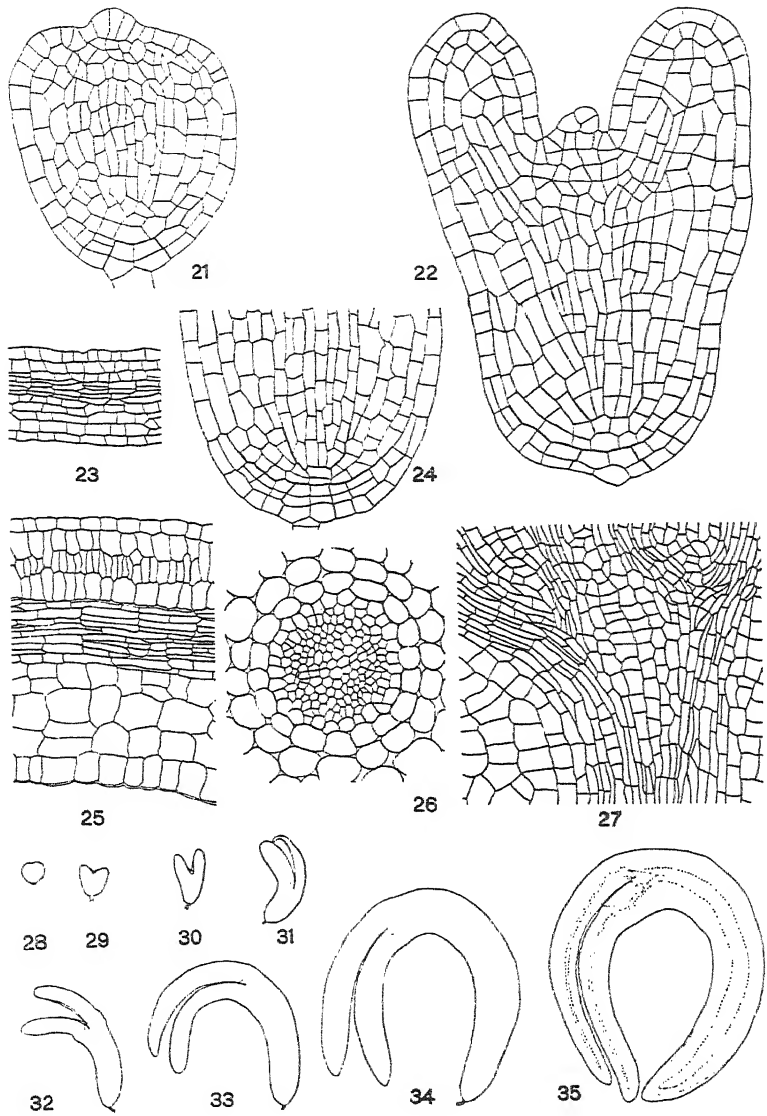
Natural distribution of Rhododendron maximum in New Jersey[1]

ERNEST L. SPENCER

(WITH ONE TEXT FIGURE)

INTRODUCTION

In sections of northern New Jersey one scarcely fails to notice *Rhododendron maximum L.* or Great Laurel, growing rather sparsely in some places but very extensively in others. *Rhododendron maximum*, a member of the Ericaceae, is one of our most beautiful plants. This woody shrub with its evergreen leaves and showy white or light pink flowers often reaches a height of from six to ten meters.

Why does this shrub grow so luxuriantly in the natural state but often lose its lustre and die when transplanted? This question has prompted the study of rhododendron in its natural habitats in New Jersey in an endeavor to ascertain what factors appear to be involved in its distribution.

The data here presented were obtained from 36 stations. A few stations may have been overlooked, but every stand which has been reported in the literature by Britton (1889) and Stone (1910), as well as many previously unrecorded stands, the locations of which were found with the help of local guides, were very carefully studied. The stations, with the exception of Sicklerville in the southern part of Camden County, are confined very largely to the northern and western areas. Rhododendron appears to be missing from the southern portion of the state. In the northern portion of the state, which forms a part of the Appalachian Province, are many narrow valleys and ravines, most of which run in a northeast-southwest direction. The southern portion of the state, belonging to the Coastal Plain, is relatively flat with very few hills but with many marshes bordering the stream courses. Observations were made on representative areas at each station. The map shows the locations where rhododendron was found at the time of this study.

Areas of rhododendron have been found in the following places, arranged by counties: Sussex-Wawayanda Plateau, Laurel Pond, Wallpack, Wawayanda, Sparta, Stokes Forest, High Point State Park, Montague, Flatbrookville, Dingmans Ferry and Millville; Passaic-Brown's, Moe Mountain, Uttertown, Bearfort Mountain, and Pinecliff Lake; Morris-Chatham Great Swamp, Milton and Copperas Mountain; Warren-Dunnfield, Pahaquarry, Hardwick and Blairstown; Hunterdon-Ramseysburg,

401
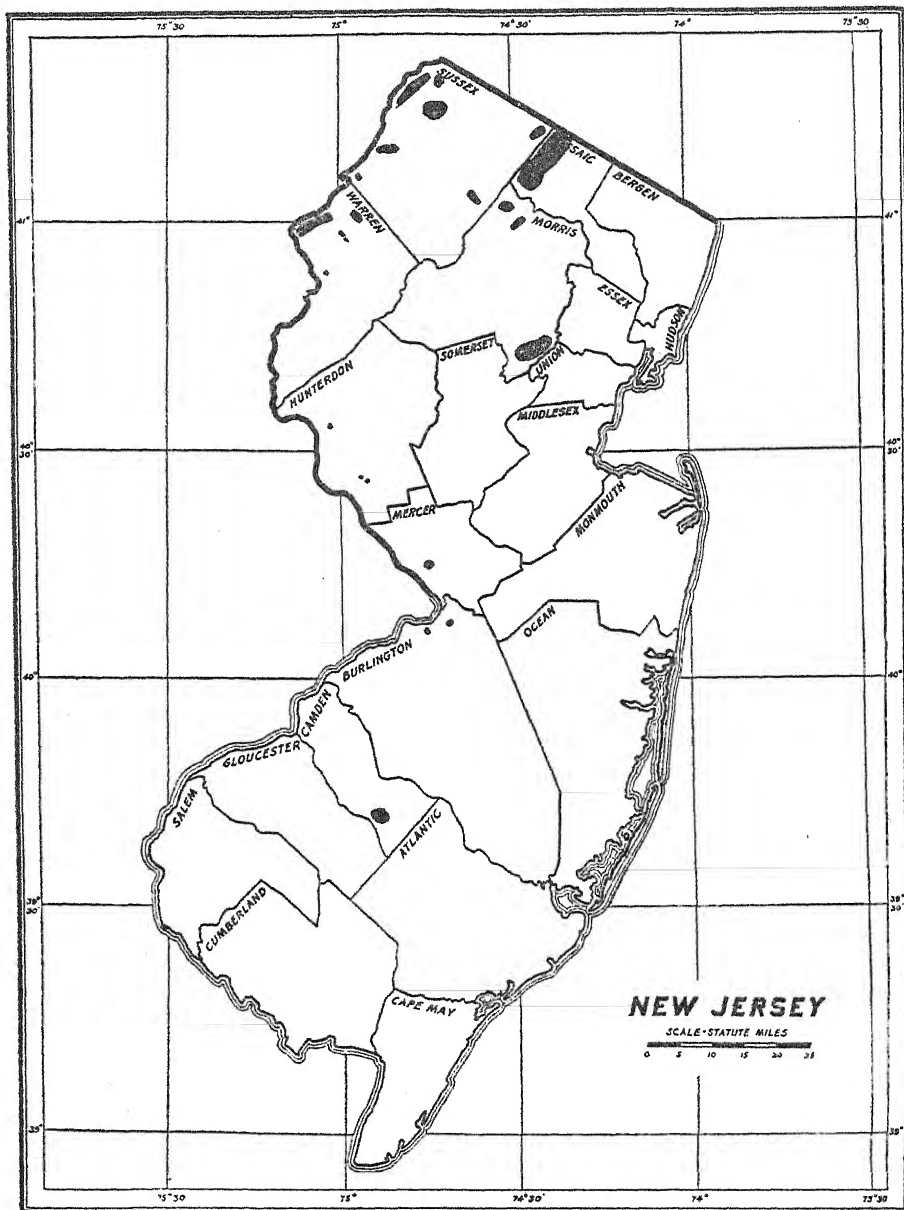
Outline map of New Jersey showing the regions where
Rhododendron maximum was found in the State

Stockton and Frenchtown; Mercer—Washington Crossing; Burlington—
Bordentown and Kinkora; Camden—Sicklerville.

<div style="text-align:center">OBSERVATIONS</div>

Because of the complexity of the factors which must be taken into account in attempting to explain the distribution of a plant, it appears advisable to consider some of these in detail. It should be understood, however, that the distribution of a plant is ultimately determined by a combination of these factors. In such a study it is necessary to explain not only the presence but also the absence of *Rhododendron maximum* in a particular locality. For clearness, the factors involved may be divided into two groups: environmental and edaphic.

Environmental factors.

As recorded in table 1 observations on the following environmental factors were made: topography, exposure, shade, proximity to water, depth of leaf mold, and drainage.

The data dealing with the topography of the stations where rhododendron grows appear at first sight to be inconsistent. A more careful study, however, reveals the fact that of the 29 principal stations, nine are in ravines, nine on hillsides or rocky cliffs, six on the banks of brooks, and five in swamps. The topography of these 29 stations is quite similar. With the exception of the swamp stations, rhododendron was found growing most luxuriantly in hemlock ravines.

This study shows that the manner of exposure is a factor of great importance to the distribution of rhododendron. Of the 29 principal stations all but five face to the north or northwest. These five exceptions are more or less flat areas; their lack of definite northern or northwestern exposures is probably compensated for by shade and humidity.

Observations made at Sparta, Wallpack and Brown's show to some extent the great significance of the exposure in the natural distribution of rhododendron, other factors being similar. Sparta Glen forms a deep east-and-west ravine in which *Tsuga canadensis* predominates. On the bank with a northern exposure rhododendron grows in great abundance. On the north bank, separated from the south bank at the base by a small brook not more than six to eight feet in width, there is not a single rhododendron plant. Soil reaction tests show a similar degree of acidity on both slopes. The exposure is the only apparent factor which distinguishes the north from the south slope and which could account for the clearly defined position occupied by rhododendron in this ravine. At Wallpack and Brown's, likewise, rhododendron is found growing in greater abundance on the slopes facing the north.

TABLE 1

Environmental factors characteristic of the different stands of Rhododendron maximum in New Jersey

STATION	TOPOGRAPHY	EXPO-SURE	SHADE	PROX. TO WATER	LEAF MOLD	DRAINAGE
				FT.	IN.	
Abundant						
1. Brown's	Hemlock Ravine	N[a]	D[b]	Adja.	$\frac{1}{2}$	Good
2. Moe Mountain	Swamp	Flat	M	Adja.	3	Poor
3. Wawayanda Plateau	Cedar Swamp	Flat	M	Adja.	2	Poor
4. Chatham Great Swamp	Swamp	Flat	M	Adja.	4	Poor
5. Laurel Pond	Rocky Hillside	NW	D	Adja.	4	Good
6. Uttertown	Hemlock Ravine	NW	D	Adja.	4	Good
7. Wallpack	Hemlock Ravine	N	D	Adja.	1	Good
8. Bearfort Mountain	Rocky Hillside	N	D	Adja.	$\frac{1}{2}$	Good
9. Wawayanda	Hemlock Ravine	NW	D	Adja.	3	Good
10. Milton	Hemlock Ravine	NW	D	Adja.	3	Good
11. Sparta	Hemlock Ravine	N	D	Adja.	0	Good
12. Stokes Forest (A)	Rocky Hillside	N	M	200	1	Good
13. Dunnfield	Rocky Cliff	N	M	100	2	Good
14. High Point Park (A)	Bank of Brook	NW	M	Adja.	5	Good
15. Stokes Forest (B)	Hemlock Ravine	NW	M	Adja.	3	Good
16. Pahaquarry	Bank of Brook	NW	M	Adja.	$\frac{1}{2}$	Good
17. Montague (South)	Ravine	NW	M	200	3	Good
18. Sicklerville	Cedar Swamp	Flat	D	Adja.	5	Poor
Numerous						
19. Flatbrookville	Bank of Brook	NE	M	Adja.	1	Good
20. Dingmans Ferry	Hillside	NW	M	600	$\frac{1}{2}$	Good
21. Millville	Hillside	NW	M	600	3	Good
22. Montague (North)	Hemlock Ravine	NW	M	Adja.	1	Good
23. Stokes Forest (C)	Rocky Hillside	NW	M	750	2	Good
24. High Point Park (B)	Bank of Brook	W	M	Adja.	2	Good
25. Copperas Mountain	Rocky Hillside	NW	M	200	2	Good
26. Bordentown	Bank of Brook	N	M	Adja.	0	Good
27. Washington Crossing	Bank of Brook	N	M	Adja.	$\frac{1}{2}$	Good
28. Hardwick	Swamp	Flat	M	Adja.	5	Poor
29. Pinecliff Lake	Rocky Hillside	N	M	Adja.	2	Good
Scattered						
30. Kinkora	Steep Hillside	N	M	Adja.	1	Good
31. Ramseysburg	Hillside	N	M	100	2	Good
32. Stockton (A)	Bank of Brook	N	M	Adja.	3	Good
33. Stockton (B)	Bank of Brook	N	M	Adja.	1	Good
34. Frenchtown	Rocky Ravine	N	M	Adja.	2	Good
35. Blairstown (A)	Bank of Brook	NW	M	Adja.	1	Good
36. Blairstown (B)	Flat Woods	Flat	M	750	1	Good

[a] NW = northwest　　　　[b] M = medium
N = north　　　　　　　　　　D = dense

The sites where rhododendron grows most luxuriantly are character-ized by a dense canopy of tree tops which permits very little direct sun-light to penetrate through to the ground below. Where the shade is less dense a mixed vegetation is found associated with rhododendron. Under such conditions *Kalmia latifolia* is also abundant. In no locality was rhododendron observed growing in dry exposed areas with little shade.

It is obvious that shade has a very marked influence on the external characters of rhododendron. In extremely dense shade the plants are straggly and crooked; the leaves are confined almost entirely to the new growth at the tips of the stems; the branches rarely grow more than one or two inches in length in any one season, and the number of blooms each season is comparatively small. In the less densely shaded situations the plants are more upright with thick, compact stems; the leaves extend more or less all along the stems but are of a lighter shade of green; the branches make as much as six to eight inches of terminal growth each season, and produce many blooms. The new growing tips of these plants are larger in diameter with more red pigment than those growing in the more densely shaded areas.

In deep ravines such as are found at Sparta, Wallpack and Brown's, the humidity is very high. The air is so saturated with moisture that the foliage often remains wet until noon or later even on bright days. In these stations an extensive development of fungi, mosses and ferns is observed and it is in such stations that rhododendron is the predominant type of undergrowth when other factors allow. Not all the stations are character-ized by exceptionally high humidity, however, but this condition is al-ways noted where the growth is most vigorous and healthy.

At nearly every station rhododendron grows in very close proximity to water, usually a small brook or stream. In only three cases was the shrub found to be at a considerable distance from water. These sites, for the most part, are on rocky hillsides.

The leaf mold at the several stations shows quite a decided variation in depth. This deposit often extends to a depth of five inches. The two sites where no leaf mold is present are on very steep slopes. Without a doubt the erosion due to rain water is sufficient to remove all the leaves and partially formed leaf mold and thereby prevents the accumulation of any such material. Most of the regions which show the greatest depth of leaf mold are rather flat, thereby favoring the accumulation of leaves and their partially decomposed remains. The average depth of leaf mold at the 29 principal stations is about two inches.

There are but five exceptions to the general conclusion that good drain-age is essential for the successful growth of rhododendron. This good

drainage is due in part, undoubtedly, to the texture of the soil, most of it being stony or gravelly. Although the soil is well drained, it appears to have an adequate supply of moisture. At Moe Mountain, Chatham, Wawayanda Plateau, Hardwick and Sicklerville, rhododendron grows in swamps.

Edaphic factors.

Schimper (1898) has given the name *edaphic* to those factors dealing with the soil and its peculiarities. These factors as recorded in table 2 are soil texture and soil reaction.

Several different soil series of the stony or gravelly type seem to be well suited to the growth of rhododendron. The soil series of each station was identified by reference to the soil survey maps of New Jersey by Jennings (1911), Lee (1921), and Patrick (1917, 1919). In addition to the rocky outcrops the soil series on which rhododendron was found are Lackawanna, Hoosic, Gloucester, Penn, Collington, Culvers, Dutchess, Wallpack, and Bermudian. No *Rhododendron maximum* was found in New Jersey on soils of limestone origin.

From the data as recorded in table 2 it is quite apparent that the acidity of the soil is of considerable importance as a factor in the distribution of rhododendron. At each station the reaction of the leaf mold, of the soil to a depth of six inches, and of the soil to a depth of twelve inches was determined. This twelve inch limit was arbitrarily selected since the roots of rhododendron seldom penetrate below this depth. With respect to the leaf mold the reaction varies from pH 5.2 to pH 2.9, with an average of pH 4.0. The acidity for the first six inches of soil ranged from pH 4.8 to pH 2.9, giving an average pH of 4.0. For the second six inches the reaction ranged from pH 4.8 to pH 2.9, with an average pH of 4.2. In view of the fact that rhododendron was not found on soil with a reaction above pH 5.6, it is concluded that this plant has a natural "preference" for acid soils.

Associated flora.

In a study of the flora occurring with *Rhododendron maximum*, it may be advisable to discuss first the species, as given in table 3, which are found in most of the stations, and then to consider in detail some of the representative larger stands.

Tsuga canadensis is associated more characteristically with rhododendron than any other species of trees. There are only ten stations in which *Tsuga canadensis* is missing. At least one species of *Quercus* may be identified with all but seven stands. Among the principal species of *Quercus* are *Q. alba*, *Q. velutina* and *Q. Prinus*. Among the species of *Acer* found associated with rhododendron, *Acer rubrum* occurs most frequently, being pres-

TABLE 2

Edaphic factors characteristic of the different stands of Rhododendron maximum

STATION	SOIL TEXTURE	HYDROGEN-ION CONCENTRATION		
		LEAF MOLD	LEAF MOLD–6″	6″–12″
		pH	pH	pH
Abundant				
1. Brown's	Hoosic gravelly loam	5.1	4.8	4.7
2. Moe Mountain	Muck	3.2	3.6	4.2
3. Wawayanda Plateau	Muck	3.6	4.0	4.1
4. Chatham Great Swamp	Muck	2.9	3.0	2.9
5. Laurel Pond	Gloucester stony loam	4.0	3.9	—
6. Uttertown	Lackawanna stony loam	4.1	3.6	3.9
7. Wallpack	Rock outcrop	4.2	4.3	4.3
8. Bearfort Mountain	Rough stony land	4.7	4.3	4.1
9. Wawayanda	Gloucester stony loam	3.9	3.3	—
10. Milton	Gloucester stony loam	3.5	—	—
11. Sparta	Gloucester stony loam	—	4.7	4.8
12. Stokes Forest (A)	Lackawanna stony loam	3.5	3.7	4.0
13. Dunnfield	Rock outcrop	4.0	—	—
14. High Point Park (A)	Lackawanna stony loam	4.8	—	—
15. Stokes Forest (B)	Lackawanna stony loam	4.9	—	—
16. Pahaquarry	Lackawanna stony loam	4.9	4.1	4.4
17. Montague (South)	Hoosic gravelly loam	3.6	3.9	4.3
18. Sicklerville	Muck	3.1	3.0	—
Numerous				
19. Flatbrookville	Hoosic gravelly loam	5.2	4.1	4.4
20. Dingmans Ferry	Wallpack fine sandy loam	4.8	4.5	4.4
21. Millville	Wallpack stony loam	4.1	4.1	3.9
22. Montague (North)	Hoosic gravelly loam	3.7	4.5	4.2
23. Stokes Forest (C)	Lackawanna stony loam	5.2	4.1	4.0
24. High Point Park (B)	Lackawanna stony loam	4.3	3.9	4.1
25. Copperas Mountain	Rough stony land	4.0	3.7	—
26. Bordentown	Collington sandy loam	—	2.9	3.6
27. Washington Crossing	Bermudian silt loam	5.0	4.5	4.1
28. Hardwick	Muck	4.2	4.2	—
29. Pinecliff Lake	Hoosic gravelly loam	3.4	4.3	—
Scattered				
30. Kinkora	Collington loam	3.3	3.8	3.5
31. Ramseysburg	Dutchess shale loam	4.6	4.4	4.3
32. Stockton (A)	Penn shale loam	5.0	4.1	4.3
33. Stockton (B)	Penn gravelly loam	3.9	3.5	—
34. Frenchtown	Penn shale loam	4.7	4.4	4.3
35. Blairstown (A)	Dutchess shale loam	5.0	4.7	4.5
36. Blairstown (B)	Culvers loam	4.8	4.6	4.5
	Average	4.0	4.0	4.2
	Range {High	5.2	4.8	4.8
	{Low	2.9	2.9	2.9

TABLE 3

The relative abundance of the various species associated with Rhododendron maximum in its natural stands

STATION	RHODODENDRON MAXIMUM	KALMIA LATIFOLIA	TSUGA CANADENSIS	ACER RUBRUM	CORNUS FLORIDA	QUERCUS ALBA	QUERCUS VELUTINA	QUERCUS PRINUS	BETULA LENTA	BETULA LUTEA	FAGUS AMERICANA	LIRIODENDRON TULIPIFERA	CHAMAECYPARIS THYOIDES
1. Brown's	P	N	P	S	S					S	S	S	
2. Moe Mountain	P	N	P	S	S					S	S		
3. Wawayanda Plateau	P		P	S		S			S	S			N
4. Chatham Great Swamp	P	N		S	S	S			S		S	S	
5. Laurel Pond	P		P	S						S	S		
6. Uttertown	P	N	P	S	S					S	S		
7. Wallpack	P	N	P	S	S	S			S				
8. Bearfort Mountain	P	N	P	S	S	S				S			
9. Wawayanda	P	N	P	S	S					S			
10. Milton	P	N	P	S	S	S				S			
11. Sparta	P	N	P	S		S			S	S			
12. Stokes Forest (A)	P	N		S			S			S			
13. Dunnfield	A	S	P	S	S		S		S				
14. High Point Park (A)	A	N	N	S	S	S	S	S	S				
15. Stokes Forest (B)	A	N	P	S			S	S	S	S		S	
16. Pahaquarry	A	N	S	S	S	S		S	S			S	
17. Montague (South)	A			S		N	S	S					
18. Sicklerville	P			S		S	S						P
19. Flatbrookville	N	N	P		S	S	S	S		S		S	
20. Dingmans Ferry	N	N	S	N	S	S	N	S	S			S	
21. Millville	N	A	N	S	S			S	S				
22. Montague (North)	N		N	S			N					S	
23. Stokes Forest (C)	N	N	P	S	S	N	S	S	S	S		S	
24. High Point Park (B)	N	A	N	S			S	S	S	S			
25. Copperas Mountain	N	A	S	S			S	S	S				
26. Bordentown	N			S	S			S			S	S	
27. Washington Crossing	N			S	S								
28. Hardwick	N	N	S	S	S	S	S	S	S				
29. Pinecliff Lake	N	N	N	S	S			P			S		
30. Kinkora	S			S	S	S	S		S		S	S	
31. Ramseysburg	S	N	N			S			S				
32. Stockton (A)	S			S	S				S				
33. Stockton (B)	S		N	S			N						
34. Frenchtown	S		N	N		S	N						
35. Blairstown (A)	S	N		S	S	S		S	S	S		S	
36. Blairstown (B)	S	N		N		S				S			
Total	36	25	26	34	22	21	15	15	14	14	10	9	2

P=predominant, A=abundant, N=numerous, S=scattered.

ent in 34 stations. *Acer saccharum* and *A. pennsylvanicum* are also found with several of the stands. *Cornus florida, Betula lenta* and *B. lutea* are present frequently, as well as scattered groups of *Liriodendron tulipifera, Fagus americana, Pinus Strobus,* and *Chamaecyparis thyoides.*

Very few different species of shrubs are present in many of the stations. *Kalmia latifolia* thrives in all but eleven of the stations where rhododendron is found. In a few of the larger areas rhododendron is the only shrub present. Isolated groups of *Viburnum,* usually *V. acerifolium, Hamamelis virginiana, Clethra alnifolia,* and *Vaccinium pennsylvanicum* are found. With the exception of the mosses and saprophytic fungi, there appears to be very little characteristic ground vegetation.

For a more detailed account of the vegetation associated with rhododendron at the different stations, it may be advisable to select a few typical sites rather than to discuss each stand separately.

At Brown's is found a typical ravine with a true hemlock formation. This ravine, which extends in a northeast to southwest direction, has a small brook with high slopes on either side. The soil here is described as rough, stony land of the Hoosic series with good under-drainage. In addition to the vigorous growth of rhododendron at the bottom of the ravine there is a stand of *Tsuga canadensis,* with only a few scattered specimens of *Fagus americana* and *Acer rubrum.* These trees are able to withstand the dense shade of the hemlock, in which rhododendron thrives. In regard to the slopes it is immediately apparent that the vegetation of one slope is different from that of the other. On the slope facing northward are found *Rhododendron maximum* and *Kalmia latifolia,* thriving beneath the dense canopy of the hemlock. This association extends far up the slope. On the opposite slope with a southern exposure a different condition is encountered. Here the forest is more of the maple-beech-hemlock type, made up of *Acer rubrum, Fagus americana* and *Tsuga canadensis,* with some *Cornus florida, Betula lutea* and *Liriodendron tulipifera.* Rhododendron, as well as hemlock, disappears a short distance up this slope.

At Wallpack similar conditions with respect to exposure prevail. At the bottom of the ravine there is a hemlock formation with an undergrowth consisting almost exclusively of *Rhododendron maximum.* On the rocky cliffs along the brook, which extends up through the ravine, are found associated with the hemlock, as secondary species since they are tolerant of shade, *Betula lenta, Acer rubrum, A. pennsylvanicum, Cornus florida,* and *Quercus alba.* As the stand of trees thins out *Kalmia latifolia* makes its appearance. On the slope facing northward is found an abundant growth of rhododendron, whereas on the opposite slope this species is absent, a

condition similar to that observed at Brown's and apparently due to the same causes.

At Dunnfield rhododendron grows in a different type of topography. Throughout the entire length of the Delaware Water Gap the rhododendron is very prominent, growing in great abundance on the rocky cliffs overlooking the Delaware River to the northwest. Here the forest is of the hemlock-deciduous type with *Tsuga canadensis, Acer rubrum, A. pennsylvanicum, Cornus florida, Quercus Prinus,* and *Betula lenta.* The cliffs are very steep and rough and give rise to little streams of water which run as from springs. The vegetation in general is quite straggly and crooked, as though subjected to severe winds.

On Moe Mountain another condition may be observed. At the top of the mountain is a large swamp in which rhododendron is very abundant. Associated with it and forming a rather open type forest is *Tsuga canadensis* and *Betula lutea.* Here the rhododendron appears very vigorous, forming a somewhat dense thicket of undergrowth. Along the margins of the swamp together with the extensive development of rhododendron, are *Quercus Prinus, Cornus florida, Kalmia latifolia* and *Myrica asplenifolia.* On the slopes arising from the swamp the same abundant growth of rhododendron as at Brown's and at Wallpack was observed on the slope facing northeast, but none at all on the opposite slope. North of the swamp both hemlock and rhododendron disappear at about the same elevation.

In a cedar swamp at Sicklerville, the southernmost station found in New Jersey, there is a very exceptional colony of rhododendron. Stone (1910) describes this station as follows: "The white cedars rose on every hand like tall columns, their dense tops shutting off much of the light, and under them, with tangled and twisted trunks and branches, grew the Rhododendrons, the masses of white blossoms standing out conspicuously against the dark leaves and the general gloom. The high humidity, the absolute lack of motion in the air, and the low basin-like character of the spot made it extremely oppressive and the atmosphere seemed fairly reeking with moisture. I have suffered from excessive perspiration in the *Rhododendron* thickets of the Alleghenies much as I did that day (July 9, 1910) in the cedar swamp, and perhaps the similarly humid conditions are what the plant needs." The absence of *Tsuga canadensis* is very conspicuous.

Seedlings. The seedlings of *Rhododendron maximum* are found in only a very few stations. There are very extensive stands of healthy seedlings at Moe Mountain on the elevated margins of the swamp, at Wallpack in the upper ravine, at Stokes Forest on the partially exposed hilltop, and at Chatham on the small knolls in the Great Swamp.

DISCUSSION

The results of these observations indicate that some of the factors studied seem to be more significant than others. Of these factors there are three which warrant further consideration: (1) soil reaction, (2) exposure, and (3) seed germination. The question of the relative importance of soil reaction and exposure in this connection is still open to discussion. The data already presented have shown that one cannot be separated from the other for it is the apparent combination of both these factors which seems to restrict the natural distribution of rhododendron.

If it is justifiable to draw conclusions from the observations made at 36 stations, it is evident that rhododendron "prefers" an acid soil. Whether or not this is a limiting factor in the distribution of rhododendron is hard to say, for this apparent "preference" has not been fully demonstrated as yet by experimental evidence. Several tentative explanations for this condition have been advanced by various workers. The acid reaction may render available some elements such as iron, which in small quantities are required for growth. Unpublished experimental evidence with solution cultures (Spencer 1932) has shown that an acid medium is essential only in rendering available some nutritive elements which are insoluble in a neutral or alkaline medium. In regard to soils, however, the experimental evidence is still too superficial to warrant drawing any definite conclusion as to the manner in which an acid reaction may function. Perhaps the same symbiotic relation, which has been demonstrated by Dufrenoy (1917) and Rayner (1923) to exist between other members of the Ericaceae and mycorrhiza, exists also between these organisms and rhododendron. If this is the case, an acid reaction may favor increased fungal activity, whereas an alkaline medium may retard its development. The fact that rhododendron is not found on the limestone soils south of Vernon on the northwest slopes of Wawayanda Mountain and similar locations in New Jersey, where other factors for the natural development of this species are apparently favorable, is evidence in support of the theory that soil acidity is an important factor in the distribution of rhododendron.

The importance of a proper exposure is very well brought out by the data already presented. The fact that no stand of rhododendron was found with a southern exposure may be based on the environmental characteristics of both the northern and southern exposures. The factors involved are undoubtedly light intensity, temperature, and humidity. On the northern exposure the light intensity is naturally lower than on the southern because the direct rays of the sun reach it at a more acute angle and for a shorter period each day. As a result of this shorter exposure to direct sunlight the temperature is normally lower. The humidity, on the other hand,

is higher since less evaporation occurs. All three of these factors are favorable to the growth of rhododendron. Winter injury is undoubtedly a significant factor in the distribution of rhododendron since it is a matter of common observation that this type of injury is much more prevalent on the southern exposure than on the northern. This is due to the frequent freezings and thawings on the southern exposures, a condition known to be quite injurious to all but the most hardy types of vegetation.

Several interesting observations were made concerning the manner in which rhododendron reproduces in the wild. It has been demonstrated experimentally by seed germination tests that the seeds are viable. Data obtained at the various stations indicate that the seedlings are highly specific in their environmental requirements. These requirements appear to be (1) a relatively high humidity, (2) a moderate exposure such as is offered by a lightly wooded forest, and (3) a soil reaction between pH 3.5 and 5.0. It is probable that in very dense shade the young seedlings cannot synthesize adequate carbohydrates to carry them through the first winter. It may also be that germination is retarded to such an extent in these areas by the lower temperature that the seedlings are not sufficiently developed at the end of the growing season to withstand the severe conditions of winter. Evidently rhododendron now growing in the dense shade of the hemlock started while these trees were still small. A count of the annual rings at the base of several of these shrubs showed that many of these larger rhododendron plants are at least 65 years old.

From the data presented it appears that the conditions under which rhododendron thrives are quite similar to those required by *Tsuga*. This undoubtedly accounts for the close association between these two species. Both species appear to thrive in the same type of environment. Harshberger (1911) describes the hemlock as a tree which thrives on the rocky sides of mountain gorges, or a rocky hillside overlooking a stream. Occasionally it appears in a deep forest on the flat ground by a stream. It grows on the slopes facing the north rather than on the southern slopes and hilltops. These conditions coincide with the apparent natural conditions required by rhododendron. The *Tsuga* has been found, however, in limestone soil in New Jersey, whereas rhododendron has never been found on such soils.

SUMMARY

1. In the State of New Jersey 36 natural stands of *Rhododendron maximum* were located, mostly in the northern and western regions of the state. In five localities the shrub grows in swamps: at Moe Mountain, Waway-

anda Plateau, Chatham Great Swamp, Hardwick, and at Sicklerville, the latter being the southernmost station in the state.

2. The distribution of rhododendron seems to be governed by its specific topographical requirements rather than by climate. It appears to prefer ravines or rocky hillsides although several stands were found along the banks of small brooks.

3. In every station rhododendron grows on acid soil and never on limestone soil. The soil reaction of the several stations is decidedly acid, the range extending from pH 5.2 to pH 2.9.

4. The significance of exposure is well brought out, especially by the stands situated in ravines. In these stations there is an extensive development of rhododendron on the slopes facing north, whereas on the opposite slopes the shrub is absent or restricted to the base of the slope. None of the 36 stations has an exposure to the south.

5. The most luxuriant growth of rhododendron is noted in localities characterized by dense shade and high humidity.

6. In New Jersey rhododendron is commonly associated with *Tsuga canadensis* and *Kalmia latifolia*.

7. Young seedlings were found in only five of the 36 stations where the larger plants are now growing. Inasmuch as germination tests showed that seeds are viable, it is evident that the seedlings themselves must be highly specific in their environmental requirements. The factors involved appear to be humidity and light intensity as well as soil reaction.

The writer wishes to acknowledge the assistance of Dr. J. A. Small and Mr. O. W. Davidson in making the observations, the financial support of Mr. W. P. Jenks of Morristown, New Jersey, and the criticisms of Dr. J. W. Shive and Dr. M. A. Chrysler in the preparation of this manuscript.

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The development of the ascocarp in two species of Thielavia

C. W. Emmons

(WITH ONE TEXT FIGURE AND PLATES 27 AND 28)

The members of the medical profession, in their studies of skin diseases especially, have accumulated much knowledge regarding species of fungi parasitic on man. Forms causing thrush, ringworm, sporotrichosis, and coccidioidal granuloma, are among those well known to the medical mycologist, but not always so familiar to those botanists concerned purely with problems of plant pathology or with fungi as a whole. There are in human pathology, just as in plant pathology, cases where it is difficult to say whether the trouble in question is primarily due to the particular fungus isolated, working as a parasite, or whether it may not simply be aggravating the original trouble in a secondary capacity. The tendency in former years has been for medical mycologists to be rather conservative and to disregard fungi other than those long known to be primary parasites, the effects of which present definite clinical pictures. More recently they have been studying culturally and experimentally those fungi occupying the border line between parasitism and saprophytism. One may cite cases where the spores of fungi familiar to the botanist, such as *Puccinia graminis*, *Penicillium glaucum*, *Alternaria Mali*[1] and others, have been proved to be the cause of asthmatic attacks in certain individuals. It is now conceded that certain cases of ear and lung troubles are due to infection by species of *Aspergillus*.

Such lines of work call for much more extended knowledge of those fungi, not only on the part of those interested in human diseases, but on the part of the botanist as well. A survey was recently organized by Dr. R. M. McLaughlin of the College of Physicians and Surgeons, Columbia University, with the primary object of learning to what extent certain groups of college students were infected with the fungi which cause ringworm of the foot. In this survey it was planned to obtain cultures, not only from those individuals with clinical lesions, but also from those who appeared to be normal. The fungi appearing in these cultures included forms known to be pathogenic, and many which probably had no etiologic significance. Most of these latter were undoubtedly represented in the lesions or on the skin merely by a few air borne and ungerminated spores which grew as soon as planted upon the culture medium. A study of these cultures has resulted in the discovery of a number of interesting forms, among which was a new species of *Thielavia* isolated by Dr. McLaughlin

[1] Hopkins, J. G., R. W. Benham, and B. M. Kesten. 1930. Asthma due to a fungus—*Alternaria*. Journ. Amer. Med. Assoc. 94: 6–10.

from the normal skin of a foot. He has kindly permitted the author to make a special study of this fungus which is considered to be a saprophyte and no great importance is attached to its source, although related forms are met with frequently as contaminants of cultures similarly made. The studies reported here were all made from strains derived from single spores.

In an earlier paper[2] I have given a brief account of *Thielavia terricola*. Further study has seemed to show that the ascogenous hyphae of that species produce croziers from the penultimate cells of which the asci develop. Some of the salient feature of its development are to be mentioned in this report which is devoted principally to a description of another species of *Thielavia* mentioned above and hitherto undescribed, although it is apparently closely related to *T. terricola*. This relationship is manifested by similarities in the manner of growth in the early stages of ascocarp formation, in the character of the mature ascocarp, and in the appearance of asci and ascospores. In the second species, however, the ascogenous hyphae develop no croziers and there is apparently no nuclear fusion in the ascus. One or the other or both of these remarkable features have been reported in other groups of fungi; the interest here lies in the fact that while one species of *Thielavia* goes through the usual stages in the formation of ascospores, a second closely related species has a very much shortened life history.

THIELAVIA TERRICOLA (GILMAN AND ABBOTT) EMMONS

The ascocarp of *Thielavia terricola* develops from a hyphal coil. The coil as well as the hypha which bears it and the hyphae which soon surround it are somewhat difficult to distinguish even when stained with aceto-carmine. There does not appear to be any antheridium. Single spore cultures produce ascocarps. The coil soon becomes surrounded by an envelope of hyphae, but it remains visible through these as a deeply staining structure made up of from one to three cells. The coil grows as the young ascocarp develops and there is an increase in the number as well as in the size of the cells. It soon gives rise to a branching system of ascogenous hyphae. The asci appear to develop from the penultimate cell of a crozier and nuclear fusion occurs at the very beginning of ascus formation. Fusion of the ultimate and the antepenultimate cells could not be demonstrated. There is no uniformity in the orientation of the ascogenous hyphae and asci. The former grow out from the coil which is located at a point near the center of the ascocarp and the asci may point in any direction. This arrangement corresponds in general to that in *Microascus trigonosporus* and

[2] Emmons, C. W. 1930. *Coniothyrium terricola* proves to be a species of *Thielavia*. Bul. Torrey Bot. Club. 57: 123–126.

M. intermedius[3] except that in *Thielavia terricola* the ascocarp is smaller but the asci are larger, and consequently the radial development of the system is less noticeable. The first asci to mature are near the center of the cleistocarpous fruiting structure, and in a maturing ascocarp, ascogenous hyphae can be found only next to the perithecium. No open central cavity forms but the nurse tissue is destroyed lysigenetically as the fertile hyphae and asci advance. Three nuclear divisions occur and eight spores are cut out. The ascospores are elliptical with a germ pore at only one end.

Thielavia Sepedonium sp. nov. Emmons.

Mycelio homothallico; perithecio globoso, 70–150μ diametro, pariete exteriori olivaceo; ascis ovoideis, 17–30μ, e ramis lateralibus hypharum asciferarum orientibus, sine nucleorum conjugationibus, 8–sporis; ascosporis ellipticis olivaceis, 7–10×14–19μ, poro germinali ad vertices ambas.

Conidiis sphaericis, interdum ovoideis, 7–10μ diametro, tuberculato-papillatis, singulatim vel in catenis brevibus ad conidiophoros ramosos proventis.

Thielavia Sepedonium is so much like *T. terricola* in the general appearance of the mature ascocarp, asci, and ascospores that the advisability of describing it as a different species was at first questioned. However it grows more rapidly and luxuriantly than *T. terricola;* it has a conspicuous conidial stage; and there are very important differences in the ascocarpic development, in the ascospores, and in the perithecial wall cells. The character of the conidia would place this fungus in the genus *Sepedonium* Link, of the Fungi Imperfecti. Of the species of this genus it most closely resembles *S. albo-luteum*, but it differs from that species in important respects noted in the description. The perfect stage, when present, should determine the taxonomic position and the name of a fungus, and the ascocarp which is a prominent feature of this fungus is that of a *Thielavia*. The specific name *Sepedonium* is proposed here in order to suggest the type of its conidial stage.

Thielavia Sepedonium develops rapidly upon cornmeal agar with the formation of a scanty gray mycelium. Within four days at 30°C, in monospore cultures, ascocarps are visible as tiny black spots on the surface of the agar, and by the fifth day many of the asci contain spores. As in many ascomycetes, the ascocarps form more quickly and in greater abundance on plate cultures of cornmeal agar if inoculations are made at several points. On dextrose and other sugar media there is a stronger development of aerial mycelium which becomes golden yellow with the production of great masses of conidia, and finally grayish over most of the colony with

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[3] Emmons, C. W., and B. O. Dodge. 1931. The ascocarpic stage of species of *Scopulariopsis*. Mycologia 23: 313–331.

the formation of ascocarps. The conidia are borne upon branched conidiophores (plate 27, a–e). The spores arise from swollen portions of the conidiophore (plate 27, c), which swellings, in many cases at least, in turn become conidia. The conidia appear to be solitary, but short chains sometimes form. The conidium is at first borne upon a little stalk and is smooth. Later, as the spore increases in size the stalk disappears and the surface becomes covered with tuberculate thickenings. The spores are spherical, 7–10μ in diameter, or sometimes egg-shaped and up to 8$\times$12μ in size.

The ascocarp develops from a hyphal coil (plate 27, f–i). No antheridium is present. The ascocarp is spherical, 70–150μ in diameter, and without an ostiole. The perithecium, the wall portion of the ascocarp, is composed (a) of a single layer of pigmented cells whose outer walls are deeply sculptured (plate 28, d) and (b) two or three layers of thin-walled flattened cells. At the center of the young fruit body one finds a number of pseudoparenchymatous cells which are eventually destroyed as the asci develop (plate 28, h). The asci, about 17$\times$30μ, arise as side branches on the ascogeneous hyphae. Each ascus contains eight ascospores which are elliptical, darkly olivaceous, 7–10$\times$14–19μ, with a germ pore at each end (plate 27, j) as contrasted with the ascospores of *T. terricola* which have only one germ pore. They remain uninucleate until germination.

In the development of the ascogenous hyphae there is at no stage any suggestion of a crozier. The growth is straight out from the original coil (text fig. 1 and plate 28, h). Each cell of the ascogenous hyphae is uninucleate except the tip cell which, just before cell division in the course of hyphal growth, becomes binucleate. Cells which are about to form branches from which asci are to be cut are also binucleate, but the ascus cell has only one nucleus when it is cut off (plate 27, l). Growth is apical as is clearly shown by the progressive development of asci along an ascogenous hypha (text fig. 1), and binucleate tip cells are occasionally seen. The ascogenous hyphae branch freely at first and binucleate cells are sometimes found at the base of a young branch. The young branch is initiated before nuclear division; after nuclear division one nucleus passes into the branch and a wall is laid down. The ascus arises in the same manner as a branch (text fig. 1 and plate 27, l), and in some cases it is difficult to be sure whether one is observing a young branch or a young ascus. In most cases it is possible to tell by noting the stage of development of the ascogenous hypha and of the asci arising from the older cells of the ascogenous hypha. If the ascocarp is well developed and ascogenous hyphae have penetrated to all parts of its interior, and if several nearly mature asci are present, further branching of the ascogenous hyphae does not occur.

The young ascus first appears two or three cells distant from the tip

(text fig. 1) and the general appearance is quite different from what one finds in *T. terricola* where the ascus appears to arise from the penultimate cell of a crozier. In *T. Sepedonium* one of the daughter nuclei passes into the young ascus (plate 27, l) which is cut off by a wall. Ascus and nucleus increase rapidly in size, but there is no preliminary binucleate stage or nuclear fusion. When the ascus reaches its mature size there are the three usual nuclear divisions. Many mitotic figures of each of the three nuclear divisions have been secured. The chromosome number seems to be four. Each of the nuclei now cuts out a spore by free-cell formation. Many preparations of a later stage show the nucleus attached to the spore wall by a long beak as described by Harper[4] for the powdery mildews. Later the nucleus rounds up at the center of the spore. The spore, which is at first spherical, later becomes ellipsoidal and it has a germ pore at each end (plate 27, j). It remains uninucleate until germination begins.
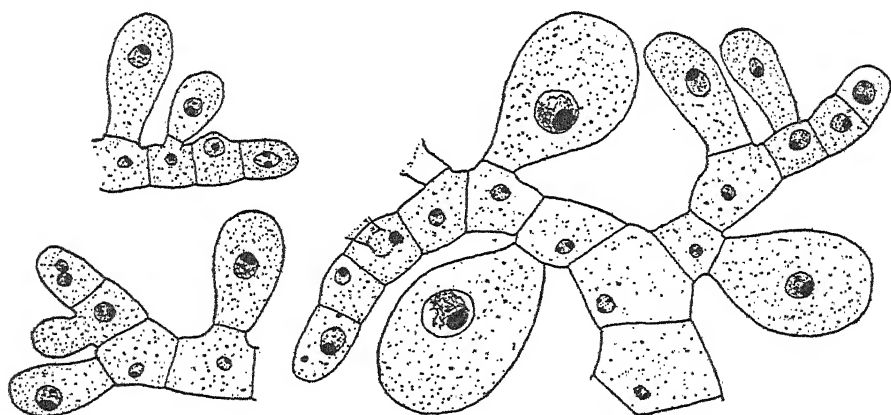
Fig. 1. Stages in the formation of the asci of *T. Sepedonium*.

The remarkable and interesting cytological features in the life history of *T. Sepedonium* are the lack of crozier or ascus crook, and the absence of a nuclear fusion in the young ascus. While the crozier can not be demonstrated in certain ascomycetous forms the nuclear fusion in the ascus is a commonly and easily observed phenomenon which is usually thought of as being universal among the higher ascomycetes. No nuclear fusions are reported to occur in some of the reduced forms such as the 4-spored yeasts and species of Endomycetaceae. It seems probable that an adequate study of many of the reduced forms among the Plectascales will show still other species where crozier formation and nuclear fusion are dispensed with.

[4] Harper, R. A. 1895. Ueber das Verhalten der Kerne bei der Fruchtentwickelung einiger Ascomyceten. Jahrb. f. Wiss. Bot. 29: 655–685.

If a crozier is present in the mildews it is in a reduced form and it seems quite certain that in some species it is lacking. However the nuclear fusion in the ascus is well known since Harper's[4] work on these forms. Wingard[5] in a study of *Nematospora Phaseoli*, the cause of a spot disease of the lima bean, found no nuclear fusion in the ascus. The only nuclear fusion known for other yeasts is that between the nuclei of the copulating cells in such forms as *Schizosaccharomyces octosporus*, and corresponds therefor to the first nuclear fusion in such forms as the mildews.

Among the Basidiomycetes there are several species where basidia form only two basidiospores and no nuclear fusion is known to occur. In *Caeoma nitens*[6] and *Endophyllum Euphorbiae-sylvaticae*[7] the nuclear fusion which usually precedes the formation of the promycelium in the rusts is lacking.

SUMMARY

Cytological data are given for two species of *Thielavia*. *T. Sepedonium* is described as a new species. It forms its asci as simple side branches from the ascogenous hyphae without crozier formation and without nuclear fusion in the ascus. *T. terricola* resembles *T. Sepedonium* superficially but in the former the asci appear to arise from the penultimate cell of a crozier which is binucleate.

I am indebted to Dr. B. O. Dodge for assistance and advice during the course of this study, and to Prof. R. A. Harper for assistance in the interpretation of the cytological details.

[5] Wingard, S. A. 1925. Studies on the pathogenicity, morphology, and cytology of *Nematospora Phaseoli*. Bul. Torrey Bot. Club. 52: 250–290.

[6] Dodge, B. O. 1924. Uninucleate aecidiospores in *Caeoma nitens* and associated phenomena. Journ. Agr. Res. 28: 1045–1058.

[7] Moreau, Mme. F. 1914. Les phénomènes de la sexualité chez les Urédinées. Botaniste. 3: 145–284.

Explanation of plates

PLATE 27

Thielavia Sepedonium

a-e, conidiophores and conidia.

f-i, ascogonial coils.

j, germinating ascospore.

k, young ascocarp showing ascogonium with uninucleate cells.

l, ascogenous hyphae bearing young asci.

PLATE 28

a, ascospores of *Thielavia Sepedonium*.

b, ascospores of *T. terricola*.

c, wall cells of the perithecium of *T. terricola*.

d, wall cells of the perithecium of *T. Sepedonium*.

e, young ascocarp of *T. Sepedonium*.

f, conidia of *T. Sepedonium*.

g, aceto-carmine preparation of crushed mount of ascogenous hyphae of *T. terricola*.

h, section of ascocarp of *T. Sepedonium*.
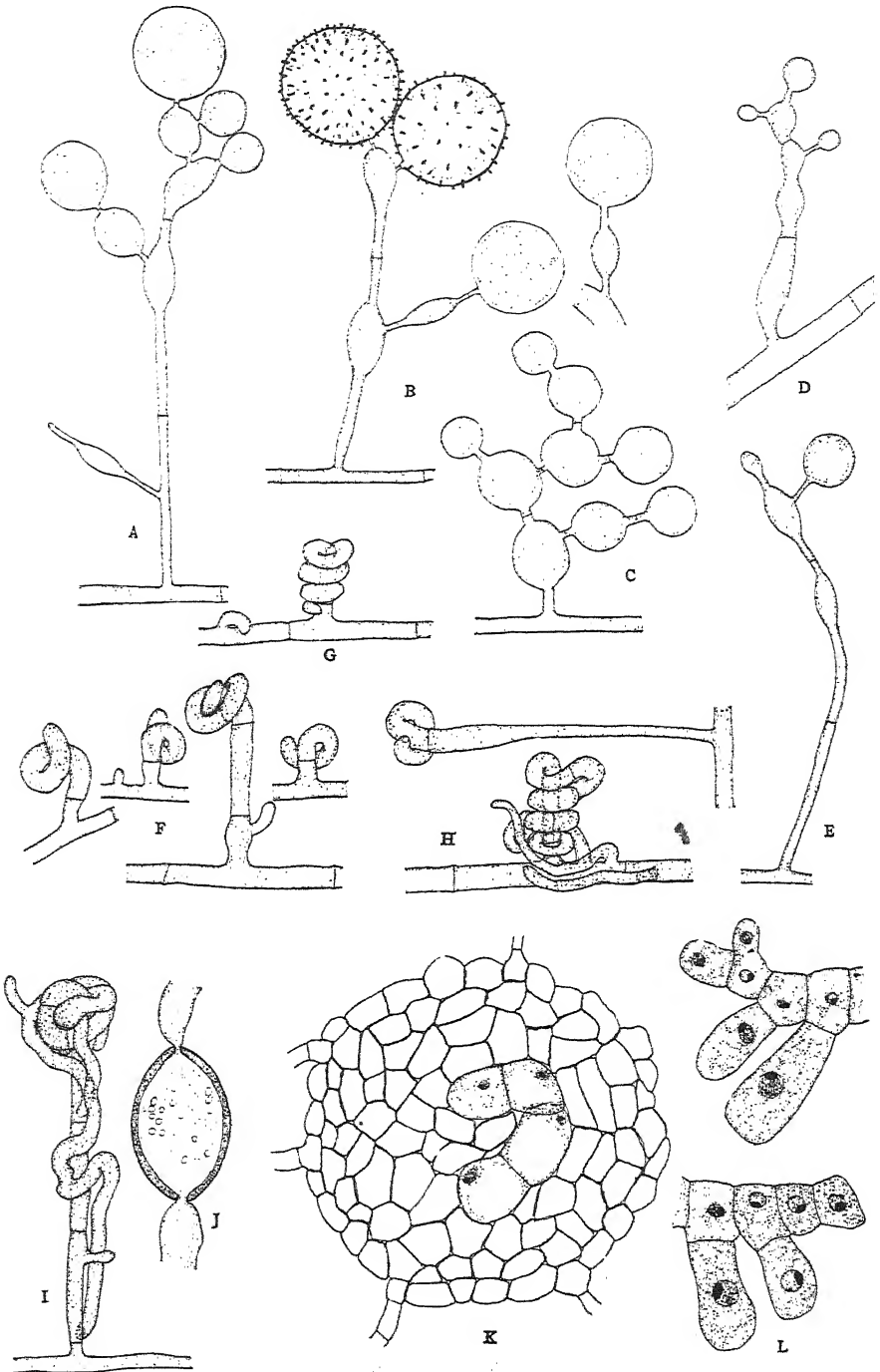
EMMONS: THIELAVIA

Regeneration in a sweet cherry leaf

V. A. Young

(WITH PLATE 29 AND ONE TEXT FIGURE)

Much has been written relative to the underlying causes of regeneration in plants, but as yet no general definition or theory has been advanced which is wholly accepted by workers as an explanation for such phenomena. Among the investigators who differed widely as to the definition of regeneration as applied to their respective problems, certain definite groups stand out quite distinctly. One of these groups includes Prantl (1874), Němec (1905), and Pfeffer (1905), who contended that regeneration is the formation of a new part or parts exactly alike in number and position of the organs injured or removed. Another group of workers, Vöchting (1878), Goebel (1902), Morgan (1901), and Klebs (1908), consider regeneration to be the development of additional organs from dormant buds present before an injury occurs. Miss Kupfer (1907), one of the more recent investigators, suggests that the term regeneration be limited to those cases in which an organ is formed, de novo, at a place or under conditions in which it would not normally be found.

The definition suggested by Miss Kupfer seems to cover quite adequately the occurrence of an unusual case of regeneration associated with the outgrowth on a leaf of sweet cherry (*Prunus avium* L.) brought to the attention of the writer during the early summer of 1931. This leaf (pl. 29) appeared normal in all respects with the exception of six small leaf-like structures (for convenience these structures will henceforth be called leaflets) on the lower surface.

From general observations each leaflet appeared as an individual unit, but after a careful examination with a hand lens it was obvious that each leaflet was composed of two small outgrowths extremely close to each other. A dark longitudinal line appears in the approximate center of each supposedly complete leaflet. This line represents the area separating the two leaflets. The manner in which the leaflets were attached to the main leaf was unique, each being firmly held near the inner edge and along the entire length of its blade, but free elsewhere. The specific areas from which the leaflets originated on the leaf could not definitely be determined from observations made with low magnification. The evidence obtained from these observations did, however, strongly indicate that the leaflets had their origin in the leaf veins. Such evidence was later confirmed from the studies made of microscopic sections from the areas supporting the regenerated organs. Both the leaf and the leaflets were rich in chlorophyl,

but their colors were distinctly different. The pigmentation of the leaf produced a deep brownish green color, while the color of the leaflets was a brilliant green. A pronounced differentiation in the external morphology of the leaf and leaflets was also apparent. In the former, as illustrated in plate 29, the margin of the blade is serrated while the margins of the leaflets facing each other are entire, but deeply lobed on the outer free edges. The venation also varies widely in both leaf types, the veins of the leaf radiating from the midrib, while there is no midrib present in the leaflets.

Microscopic sections were made of all leaf areas supporting regenerated leaflets. The usual histological methods were used.[1] The general anatomical structure of a cross-section of one of these areas is illustrated in figure 1 by a drawing made with a Promar drawing apparatus. The anatomy of the leaf in the region of the regeneration is highly diversified as compared with
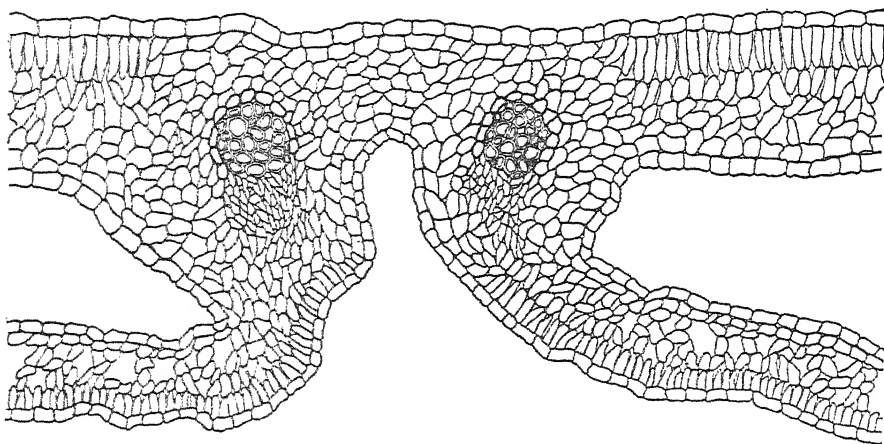
Fig. 1

the normal areas. This is due to the fact that two separate and distinct vascular systems are formed by the dichotomous branching of the vein (secondary veins) and being discontinued with the region of regeneration. The anatomical features of these secondary veins are also highly diversified as compared with the primary vein, the phloem tissue in each case being unusually large. In addition the mesophyll tissue between as well as surrounding the two veins is composed of large irregular and closely congested parenchyma, which has apparently replaced the palisade layer of the leaf directly above the two veins for some distance along the margin. One of

[1] Many helpful suggestions were offered by Dr. H. F. A. Meier, head of the Botany and Pathology Department, in the preparation of the histological material.

the undetermined anatomical complexities was the initial origin of the two secondary veins from the primary vein. All of the microscopic sections taken in the leaf tissues both near and including the region of the regenerated organs show no anatomical differences which might indicate the specific area or tissue where the division first occurred. In every section a sharp boundary separated the two secondary veins from the primary vein where a transitional area might be expected. It is highly possible, however, that a transitional area did exist in the young developing leaf when regeneration first occurred, but later the differentiation of the cells had obliterated all traces of the origin of the tissues involved. The microscopic study did, however, clearly show that the first external appearance of the regenerated leaflets was definitely correlated with the presence of the secondary veins. Furthermore the anatomical structure of the secondary veins strongly indicated that the phloem tissue was involved in the reproduction of the additional leaflets. As stated elsewhere the phloem tissue is unusually large and the cells appear to blend gradually into a system of parenchymatous tissue of the small leaflets. From such evidence one might conceive that the phloem tissue of the initial vein is the source of origin of the secondary veins. The anatomical features of the leaflets, as illustrated in figure 1, are similar to those of the leaf except that the palisade layer of the former is reversed in position with that of the latter.

Since the anatomical data discussed represent conditions found in a mature leaf supporting regenerative organs, it is only possible to postulate as to the specific cells or tissues involved in the regeneration. A young leaf exhibiting similar characteristics at a very early stage would unquestionably solve the problem. Nevertheless the data discussed above definitely indicate that regeneration may occur in plant tissues which show no evidence of external injury. Furthermore the anatomical evidence of the mature leaf does not indicate that dormant buds were present before the additional organs were formed. Moreover the evidence is quite conclusive that regeneration induces pronounced anatomical changes where it occurs, regardless of the specific cells or tissue responsible for the origin of the new organs. It is highly possible that certain physiological reactions not clearly understood play a major rôle in causing regeneration.

The literature shows that a profound interest has been aroused among biologists in the subject of regeneration. Much progress has been made in this phase of biology; nevertheless, much more is still to be accomplished before any definite theories can be formulated relative to the underlying causes of regeneration. With this realization in mind it has been the hope of the writer that the data presented might encourage other investigators to seek further for additional information relative to the complexities of

regeneration, a phenomenon more common in nature than is generally realized.

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YOUNG: REGENERATION

Field and herbarium studies, I

Louis Williams

In working up a collection of plants which the writer and Miss Rua Pierson made in and near Grand Teton National Park during the summer of 1931, attention was called to the *Phacelia* and *Corallorrhiza* as probably new. The *Eriogonum* species were received from A. O. Garrett and given to the writer by Doctor Aven Nelson for study. The following species have been carefully compared by myself, under the direction of Doctor Nelson, with material in The Rocky Mountain Herbarium.

Corallorrhiza purpurea L. Williams sp. nov. Caulis carnosus, ruber, 2 dm. altus; racemus cum 20–30 floribus; planta glabra; flores 1.5 cm. longi; labium circa 8 mm. longum, purpureum, cum 2 lobis lateralibus; pollinia 4; sepala subviridia, subaequalia; petala similia.

Scape red, fleshy, 2–4 dm. high with 2–3 membranaceous sheaths. Raceme 20 to 30-flowered, compact when young, less so with age; root coralloid; plant glabrous throughout; flowers about 1.5 cm. long; lip about 8 mm. long, purplish, faintly 3-nerved or only the central nerve visible, with a basal lobe on each side which may be bifid, there may also be some serrations between the lobes and the apex of the lip; column about 4 mm. long, to which are attached four pollinia by a central filament, two on each side of the filament, waxy, easily detached; sepals three, greenish, subequal, the lateral ones forming a short spur, which is less than 1 mm. long, faintly 3-nerved or apparently not at all; petals similar to the sepals, often tinged with purple.

This species somewhat resembles *C. Mertensiana* Bong. It differs in that *C. purpurea* L. Williams has a lobed lip which may also have some serrations, the column is shorter, and it usually has more flowers in the raceme.

Type specimen collected by Louis Williams and Rua Pierson in moist shaded situations, near Bradley Lake, Grand Teton National Park, June 22, 1931. Coll. No. 199. Type in Rocky Mt. Herb.

Eriogonum crispum L. Williams sp. nov. Perenne ligneum, ramosum, praeter 3 dm. altum, ascendens; cortex concisurus, tomentosus; folia oblonga, crenata, tomentosa infra alba, prope vel omnino glabra supra, fasciculata ad caulem veterem, alternata ad incrementum annuum; inflorescentia cymosa; involucrum circa 1 mm. longum, campanulatum, pubescens, 5–8-denticulatum, dentes subfusci; perianthum flavum, glabrum; filamentum ad basin villosum.

A coarse, diffusely branched, woody perennial. More than 3 dm. high; bark somewhat shreddy, appearing white from tomentum, probably becoming more or less glabrous with age; stems ascending; leaves short-petiolate, oblong, 2–3 cm. long, 3–7 mm. broad, crenately crisped giving the appearance of serrations, densely white tomentose below, sparingly so or glabrous above, mostly

fascicled on the older stems, alternate on the annual growth, approaching within 4–6 cm. of the inflorescence which is a multi-compound-cymose umbel; involucre about 1 mm. long, campanulate, pubescent, 5–8-toothed, tips of the teeth brownish; perianth stipitate, bright yellow; segments about 1 mm. long, equal, obtuse-ovate, glabrous; filament villose at the base, as long as the perianth.

A very pretty form of woody *Eriogonum* collected by A. O. Garrett in Cedar Canyon, Iron County, Utah, September 2, 1931. Coll. No. 6027. The specimen in hand is 3 dm. tall, the plant from which it was taken was probably 4–6 dm. or more. Type in Rocky Mt. Herb.

Eriogonum filiformum L. Williams sp. nov. Annuum ramosissimum; caulis filiformis, 1–2 dm. altus, aliquot ex caudice, glabri; nodi amplificati et angulosi; folia omnia ad basin, lamina oblonga, 1–4 cm. longa, tomentosa infra et supra prope vel omnino glabra; involucra 0.5–1 mm. longa, axillaria, pubescentia, campanulata, cum paucis floribus; pedicelli circa 5 mm. longi vel pauci sessiles in axi; lobi obtusi, breves, subrubro-gilvo ad rubidum; segmenta aequalia; bracteae squameae.

A diffusely di-trichotomously branched annual. The stems gradually diminishing in size until they are almost filiform, 1–2 dm. high; main branches several from the caudex, glabrous; the nodes enlarged and angled; leaves all basal, leaf blades 1–4 cm. long, oblong, tomentose below, sparsely so or glabrate above; petiole 2–5 cm. long; involucres 0.5–1 mm. long, axillary, pubescent, campanulate, few flowered; pedicels of the involucres mostly about 5 mm. long or a few sessile in the axis; lobes obtuse, short reddish; perianth reddish-yellow to dark red; segments equal, obtuse; bracts scale-like.

Collected west of Hawksville, Wayne County, Utah, July 23, 1931, by A. O. Garrett. Coll. No. 5975. Type in Rocky Mt. Herb.

Eriogonum Nelsonii L. Williams sp. nov. Perenne ligneum, praeter 2 dm. altum, breviter et dense tomentosum plus minus glabrescens cum aetate; folia lineari-revoluta, 0.5–1.5 cm. longa, infra tomentosa, plus minus glabra supra; petioli breves vel nulli; inflorescentia multi-cymoso-umbellata; involucrum 1–2 mm. longum, viride vel fuscum, villoso-pubescens, campanulatum, acutilobum; perianthum album cum vena viridi in quoque lobo.

A woody perennial, more than two dm. high, with shreddy bark. Densely short tomentose, more tomentose from the base toward the tip and becoming more or less glabrous with age; leaves linear-revolute, 0.5–1.5 cm. long, appearing mucronate, some of the leaves of the perennial growth fascicled, alternate on the annual and ascending within 4–8 cm, of the inflorescence, all densely woolly-tomentose on the lower side, less so or glabrous above; petiole very short or absent; inflorescence a few involucral heads (10–40) in a compound-cymose-umbel; involucre 1–2 mm. long, green or brown, villose pubescent, campanulate; lobes acute; perianth white with a green vein in each lobe; lobes ovate, 1 mm. or less long, equal; stamens almost as long as the perianth;

anthers red, nodding; filament pubescent; flowers stipitate, 4–10 in each in-
volucral head.

It is with pleasure that I dedicate this species to Dr. Aven Nelson; first
because of the generous help which he has at all times given me; secondly
because he had spent some time on the type when it was received and had
designated it as probably new.

The type specimen was collected by Ernest P. Walker, July 30, 1912,
in a dry sandy park, Geyser Basin, San Juan County, Utah. Coll. No. 368.
The co-type specimen was collected by A. O. Garrett at Cedar Canyon,
Iron County, Utah, September 2, 1931. Coll. No. 6028. Type and co-type
in Rocky Mt. Herb.

Phacelia Piersoniae. L. Williams sp. nov. Bienne erecta, 2–4 dm. alta,
sine ramis, pubescens; folia caulis petiolata, integra, lineari-lanceolata,
pubescentia; calycis lobi hirsuti, lineares, 3 mm. longi, acuti; corolla alba,
glabra, 4–6 mm. longa; inflorescentia hispido-hirsuta, scorpioidea; ovarium
hirsutum; stylus divisus ad medium.

Biennial with a short tap-root. Stems strikingly erect, 2–4 dm. high, un-
branched, only one stem from each tap-root, pubescent; cauline leaves petio-
late, entire, linear-lanceolate, tapering to the petiole and acute at the tip,
4–8 cm. long, pubescent on both sides, more so above than below, veins well
pronounced on the lower side, less so above, leaves of the preceding year form-
ing a rosette at the base of the stem, more or less pubescent; calyx lobes hir-
sute, more so on the margins than in the center, narrowly linear, about 3 mm.
long, acute; corolla white, glabrous, 4–6 mm. long, fading to ochroleucous in
drying; inflorescence hispid-hirsute, consisting of several short-peduncled
scorpioid spikes; filaments 6–8 mm. long, sparsely pilose, exserted, attached
near the base of the corolla tube, alternate with the lobes; anthers versatile;
ovary densely hirsute, ovate; style almost as long as the stamens, cleft to the
middle.

This species is probably closely related to *P. nemoralis* Greene. It re-
sembles somewhat the description of *P. leptosepala* Rydberg, which Doctor
Brand, in his monograph on the *Hydrophyllaceae*, reduces to *P. nemoralis*
Greene. It differs in that *P. nemoralis* Greene is perennial, has ascending
stems and a more or less caespitose rootstalk.

The type was collected on the STS Ranch, Moose, Jackson Hole,
Wyoming, June 26, 1931. Coll. No. 223 (Louis Williams and Rua Pierson).
Co-type collected in Grand Teton National Park, along the trail above
Bradley Lake, June 24, 1931. Coll. No. 359 (Louis Williams and Rua Pier-
son). It is dedicated to the co-collector. Type and co-type in Rocky Mt.
Herb.

UNIVERSITY OF WYOMING
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The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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Calcium and magnesium requirements of Aspergillus niger

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(WITH THIRTEEN TEXT FIGURES)

INTRODUCTION

Much research has been carried on concerning the relations of calcium and magnesium to the nutrition and various physiological processes of the lower as well as of the higher plants. It is generally agreed that magnesium in small amounts is necessary for the life of all plants, although in only slightly larger amounts it may be toxic to the higher green plants. Calcium has been found to be essential for the life of the higher green plants, but there seems to be some question as to its necessity for the lower forms.

Text books by the following authors serve as excellent sources for the literature on the nutritional requirements of the lower plants: Benecke and Jost (1924), Czapek (1920), Lafar (1911), Lutman (1929), Molisch (1920), Palladin (1926), and Pfeffer (1900). These all concur in the opinion that magnesium is necessary for the nutrition of the lower fungi and that calcium is not essential for these organisms.

A continued article by Tamiya and Morita (1929–1930) appearing in *The Botanical Magazine* of the Tokyo Botanical Society, volumes 43 and 44, gives a bibliography of *Aspergillus* from 1729 through 1928. In all, 2424 papers are listed. This gives an idea of the immense amount of work which has been done by investigators of this organism. Some of the papers which relate to the present undertaking will be cited here.

Nutrient solutions

Raulin (1869) devised a very complicated nutrient solution for fungi. It contained, among many other elements, magnesium, iron, and zinc, but no calcium. A far simpler nutrient solution was that of Pfeffer (1895). This contained, besides a source of carbon, ammonium nitrate, monopotassium phosphate, and magnesium sulphate. These salts were considered sufficient to fulfill all nutritional needs of the fungus. Calcium and iron were not ordinarily included. The same three-salt solution was used by H. Richards (1897), with sucrose as the carbon source and the addition of a trace of iron, for cultivating *Aspergillus niger*.

The question of the necessity of including iron, zinc, and other elements in the nutrient solutions for fungi has been the subject of considerable discussion. Molisch (1892) considered that iron was indispensable for the full growth of *Aspergillus niger* and that spores could not be formed in its absence. Benecke (1895) was not able to prove conclusively the neces-

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sity of iron, while Wehmer (1895) thought that iron was unnecessary for spore formation by this organism. H. Richards (1897) considered that iron was necessary in small amounts for the growth of *Aspergillus niger*. He, moreover, found that iron stimulated the growth of this organism and could be used to replace zinc for this purpose. He, as well as Buromsky (1913), tested the influence of zinc sulphate on this fungus. They both came to the conclusion that zinc does not belong to the indispensable elements, without which the fungus cannot grow, but that it belongs to the substances which stimulate if used in small quantities, but at the same time hinder sporulation. Ono (1900) and H. Richards (1899) found that zinc sulphate stimulated the growth of *Aspergillus niger* and increased the ratio of dry weight to sugar consumed (economic coefficient). Buromsky (1913) also found that zinc sulphate helped the fungus to use sugar economically. The stimulating effect of low concentrations of zinc salts on *Aspergillus niger* was again observed by Richter (1901), who maintained furthermore that copper salts in low and high concentrations always poisoned the fungus.

Coupin (1903a) said that iron, silicon, and zinc have no place in the nutrition of *Sterigmatocystis nigra* (synonymous with *Aspergillus niger*) and that zinc retards development. It was found by Javillier and Sauton (1911) that conidia were formed if iron sulphate was omitted from the nutrient solution and that large amounts of zinc sulphate caused nonsporulation. They concluded that if iron is really indispensable for the formation of spores by *Aspergillus niger*, the amount needed must be extremely small. Waterman (1912) did not consider that a high weight of mycelium is always a favorable indication of the growth of this fungus, but that the power of spore formation must be taken into consideration. He found that certain concentrations of copper sulphate, zinc chloride and sulphate increased the assimilation quotient of carbon, while the observed increase in dry weight was proportional to retarded spore formation. Very dilute zinc solutions had no effect. Copper salts in all tested dilutions counteracted spore formation.

In the work of Currie (1917) every possible precaution appears to have been taken to exclude iron, even in small traces, from the nutrient solution. This author expressed the opinion that iron is not at all necessary for the development of spores of *Aspergillus niger*. Iron added to solutions in which nitrates were used as the source of nitrogen increased the rate of metabolism and weight of mycelium. When ammonium salts were used instead of nitrates, the addition of iron was entirely without effect.

By means of autoclaving with calcium carbonate, Steinberg (1919) considered that he had removed traces of iron and zinc from his nutrient

solution. *Aspergillus niger* made no growth in the solution treated in this manner. Growth was limited when zinc and iron were added separately, but there was a marked increase when both were added together. Therefore he thought that iron and zinc were both needed by this fungus. Steinberg (1920) considered that there may be a partial replacement of iron and zinc by cobalt and uranium, if the former elements are present in not too low amounts.

Bulkewitsch (1922) found zinc sulphate to have no influence on the weight of the felt and the quantity of ammonia formed when *Aspergillus niger* was grown on a peptone medium. He concluded that the well-known growth acceleration due to this salt is specific and only occurs when a few carbon sources are used—for example, carbohydrates and similar compounds. Frouin (1923) found that the suppression of zinc in the nutritive material, if glucose is used instead of sucrose, does not diminish the dry weight of *Aspergillus niger* and that the suppression of iron increases the weight. Glucose, however, is likely to contain impurities (McHargue and Calfee, 1931). That iron seems unfavorable to proteolytic activity of the same fungus, as shown by the power to liquefy gelatine, was observed by Malfitano and Catoire (1924).

Bertrand and Javillier (1911) thought that manganese possesses a favorable influence on the development of *Aspergillus*. Bertrand (1912a) concluded that manganese determines sporulation, but that iron and zinc must also be present, the three being nutritive elements. Bertrand (1912b) thought that the very minute quantities of manganese usually found in commercial salts fulfill the requirements of the fungus for this element.

Several later papers on the heavy metals show that there is some ground for considering four of these as essential. Bortels (1927) removed traces of iron, zinc, and copper from his nutrient solution by adsorption with blood charcoal. His experiments indicated that iron and zinc were necessary for the life of *Aspergillus niger* and that iron and copper were indispensable for the black color of the spores. Metz (1930) found copper necessary for sporulation, and Wolff and Emmerie (1930) considered that this metal was necessary for growth as well as for sporulation. This is in direct contradiction of the earlier work of Richter and Waterman just mentioned, who attributed only a toxic influence to copper.

Roberg (1928) also concluded that iron and zinc were essential and that copper was needed for spore formation of *Aspergillus niger*. His illustrations of *Aspergillus* felts, which have received iron and zinc, are those of typically "stimulated" cultures; these felts appear to be heavy and wrinkled, and they exhibit subnormal spore production. This effect H. Richards (1897) considered as showing stimulation but not nutrition.

Possibly Roberg's cultures were supplied with supra-optimal concentrations of iron and zinc. It would seem that an element to be really beneficial should encourage a healthy development of spores as well as of mycelium. Roberg (1931) found that (1) zinc in small quantities is an absolutely necessary mineral nutrient for *Aspergillus niger* and for several other species of this fungus; (2) in larger quantities zinc acts as a stimulant; (3) still larger quantities act as a poison. If iron is lacking in sufficient amounts, the first unfavorable influence of zinc shows as inhibition of fructification.

Mokragnatz (1931), growing *Aspergillus niger* on Raulin's solution, found that nickel sulphate had a favorable effect on the dry weight of felts when used in low concentrations; cobalt sulphate, however, had no beneficial effect. McHargue and Calfee (1931), growing *Aspergillus flavus* on a more complicated solution than Pfeffer's (including iron and calcium), found that combinations of the optimum concentrations of manganese, copper, and zinc produced greater growth than did any one of the three or than did combinations of any two. These authors consider that in the ordinary synthetic culture solution these elements are usually present as impurities in sufficient quantities for the normal growth of the plant.

Magnesium and calcium for Aspergillus and Penicillium

Benecke and Molisch were the earliest workers to carry on comprehensive experiments with the object of discovering the relations of magnesium and calcium to the growth of *Aspergillus* and *Penicillium* in nutrient solutions. Benecke (1894a) concluded from his experiments that sulphur, phosphorus, potassium, magnesium, and iron are indispensable for the life of all plants, and that calcium is also needed by the green plants, but not by the fungi. He used *Aspergillus niger* and *Penicillium glaucum* in some experiments in which magnesium sulphate was present in the nutrient solution. The addition of 0.05 per cent of calcium sulphate did not improve the weight or conidium formation. Benecke (1895) grew *Aspergillus niger* in a basic solution containing no magnesium. He tried the effects of adding calcium nitrate, barium nitrate, strontium nitrate, magnesium sulphate, and magnesium sulphate and calcium nitrate together. Only under the last two conditions did he obtain growth resulting in spore-bearing felts. He concluded that magnesium is absolutely indispensable and cannot be replaced by calcium (also Benecke, 1894b). The latter element, if present, may be used by the fungus in an indirect manner, as possibly in the thickening of the cell wall; but it is not an integral substance for the life of the protoplasm as is magnesium. Benecke (1896) tested the effect of small amounts of magnesium sulphate on the same fungus by adding this

salt to 25 cc. of his solution (which contained ammonium sulphate as another source of sulphur) in quantities varying from 0.01 gram to 0.0000025 gram and finally none. The dry weight of fungus formed decreased in direct ratio with the decrease in magnesium sulphate. With none of this salt, the weight was very slight.

Molisch (1894a, 1894b) considered magnesium to be an essential element for fungi as well as for the higher green plants. He proved that *Penicillium sp.* and *Aspergillus niger* did not grow if magnesium sulphate was left out of the nutrient solution, even if calcium sulphate were supplied. He also concluded that calcium cannot replace magnesium and that calcium is not necessary for the growth of the lower fungi, which differ in this manner from the higher green plants.

Wehmer (1895) thought that calcium was wholly out of place in culturing fungi, but was undecided as to the necessity of magnesium. Günther (1897) found the same elements necessary for fungi as were included by Pfeffer in his solution, and decided that magnesium salts could not be replaced by the salts of calcium or related elements. Javillier (1913) considered that magnesium is indispensable for *Sterigmatocystis nigra* and that it cannot be replaced by glucinium. Coupin (1903b) found that magnesium may be used by this fungus as phosphate, sulphate, chloride, nitrate, etc.

The ratio between magnesium and phosphorus was regarded by Reed (1907) as important for the proper development of *Aspergillus niger*. Too large a supply of magnesium as compared with the phosphorus increased the weight of mycelium, but hindered spore formation. Waterman (1913), working with the same fungus, found that comparatively large amounts of magnesium checked the formation of mycelium while still larger concentrations allowed growth only after several days. He thought that very small amounts of zinc might activate magnesium. Canals (1929) decided that magnesium plays a rôle in the life of plants as important as that of carbon, hydrogen, and oxygen. He considered that it probably circulates as magnesium phosphate, which is easily dissociated. The magnesium is thus readily obtainable for making complex molecules necessary for the life of plants, such as chlorophyll in the higher plants and sucrase in the fungi. Rippel and Behr (1930) thought that the mycelium of *Aspergillus niger* contains organic magnesium compounds not soluble in acetone, and that in this respect there is a difference between the fungus and etiolated parts of green plants.

A very ingenious theory was evolved by Loew (1892, 1895, 1899, 1903, 1925) to explain the functions of magnesium and calcium in plants. He held that the element magnesium is needed to carry phosphoric acid to

the cell for the formation of nucleo-proteins and lecithin. Magnesium cannot be replaced by calcium, as this latter element cannot act in this manner. He also supposed that calcium-protein compounds enter into the composition of the nucleus and chlorophyll bodies of the higher plants and higher algae, but that the nucleus of the fungi has a different chemical composition. He thought that by placing various plants in solutions of potassium oxalate any calcium present in the cell would be precipitated. As the lower fungi and lower algae are not harmed by this treatment, Loew considered that they do not need calcium, while *Spirogyra* and many other plants are harmed and consequently do need calcium. Hori (1910), using the same method, decided that *Aspergillus niger*, *Aspergillus flavus* and *Penicillium glaucum* do not need calcium.

Robert (1911, 1912) found calcium present as an impurity in the sugar and salts that she obtained from commercial sources. She grew *Aspergillus niger* with small amounts of calcium sulphate added to Raulin's solution, which was made with materials purified until they gave no reaction for calcium with the chemical tests that she employed. *Aspergillus* grew as well with as without the addition of these small amounts, and all of the calcium added was found in the ash of the mycelium. But when very large amounts of calcium were added, the felt weighed slightly more and only eighty per cent of the calcium was found in the ash. She thought that the calcium was fixed by the oxalic acid formed and that this oxalate in the mycelium accounted for the increase in weight. Wehmer (1906) added calcium carbonate to a three-salt solution and collected many oxalate crystals from the under side of the felt of *Aspergillus niger*.

Steinberg (1919, p. 366) concluded from his experiments that calcium has no effect on the growth of *Aspergillus niger*. A series of tests performed by Buromsky (1913) with the same organism, grown in Pfeffer's solution to which calcium sulphate was added and from which magnesium sulphate was omitted, led him to conclude that calcium has no meaning as a nutrient for this fungus, since growth was very poor under these conditions, and equally so whether ammonium sulphate or nitrate was used as a source of nitrogen. He stated that magnesium serves not only as an element necessary for growth but also as a stimulant, since the dry weight and the ability of the fungus to use sugar economically were increased together by the use of this element, as is true when zinc is used. The same worker obtained very favorable results with calcium and magnesium together, but attributed these entirely to the presence of the magnesium. He also thought that ammonium nitrate is a stimulant, as is zinc sulphate.

Haenseler (1921) compared the effects of sodium nitrate and calcium nitrate on the growth of *Aspergillus niger*. The cultures with calcium gave

uniformly higher yields than did those with sodium having equivalent amounts of NO_3. Thus the calcium ion seemed better for the fungus than the sodium ion. Young and Bennett (1922) used nutrient solutions in which potassium nitrate was compared with calcium nitrate as a source of nitrogen for the growth of *Aspergillus niger* and a number of other fungi. Each solution contained another potassium salt, which supplied the essential potassium ion. They thought that calcium exerted a stimulative action on the growth of the fungi, because the calcium nitrate was more favorable than the potassium nitrate. They also considered that calcium was necessary to counteract the acidity of the solution. Contrary to the great mass of evidence cited above, they say that a salt containing calcium should have a place in the best synthetic solutions for fungi.

Coupin (1927), like Waterman (1912), cast doubt on the conclusions drawn simply from a comparison of dry weights of fungus felts. He found that *Penicillium glaucum*, grown on Raulin's solution containing no calcium, did not produce spores unless a salt of this element was added. But *Sterigmatocystis nigra* seemed indifferent to the presence or absence of calcium. Davis, Marloth, and Bishop (1928) reported that calcium increased the yield of *Aspergillus niger* and *Penicillium italicum* and that spore formation depended upon the presence of this ion. Full details of their experiments have not yet been published.

Magnesium and calcium for other plants

Mayer (1869) studied the fermentation power of yeast in nutrient solutions. His salts were fewer in number than those employed by Raulin. The mineral requirements for continued normal appearance of the yeast cells were fulfilled by potassium phosphate, magnesium sulphate, and calcium phosphate, added to sugar and an ammonium salt. He was doubtful as to whether both ions of magnesium sulphate are essential, and considered that there should be further experiments to settle the necessity of calcium.

Winogradsky (1884) decided that magnesium was absolutely necessary for the growth of *Mycoderma vini*, while calcium was regarded as useless. Molisch (1895) found that some algae behave like the lower fungi in that they can dispense with calcium, while *Spirogyra* and *Vaucheria* die if deprived of this element. Benecke (1898) concluded that these two algae must have magnesium in order to live, and that *Chlamydomonas* and *Protococcus* can live and reproduce vegetatively without calcium.

Loew (1898) thought that bacteria and yeast, since they are not harmed by neutral oxalate solutions, do not need calcium. Loew (1901, 1913, 1925) observed that *Spirogyra* was harmed by oxalate solutions and concluded that this alga needs calcium. Hori (1910) found that several of the

higher fungi would not grow in oxalate solutions; he regarded calcium as indispensable for them. Pringsheim (1926) grew various algae and mosses in solutions of sodium oxalate. He stated that it may be taken for granted that traces of calcium can be absorbed in the presence of oxalate. But his experiments led him to conclude that in general the higher algae and mosses need calcium and the lower algae do not.

Gabritschewsky (1902) did not wholly agree with Loew in regard to the relation of bacteria to calcium. He considered that the value of calcium may vary for different bacteria and expressed the opinion that certain kinds do require calcium. O. Richards (1925) found that calcium sulphate in suitable concentration gave optimum growth of yeast. Small amounts were not sufficient for optimum growth, and larger amounts were toxic.

Dunn (1921), in her study of two races of *Rhizopus nigricans* grown on a three-salt solution with dextrose and a trace of iron phosphate, found that the plus and minus strains made excellent growth if given ammonia, either with or without the addition of calcium. Calcium was not injurious, nor was an appreciable amount essential for active growth of these two races. Some calcium may have been present in the solution, but none was purposely added to it.

Lundegardh (1924) reported that calcium chloride increased the respiration of *Gibberella Saubinetii* in an acid medium, but that calcium ions had no noticeable influence in neutral solutions. He considered that calcium was not needed as a mineral nutrient for this organism.

Antagonism

Comparatively little work has been done with the lower plants on the ability of certain substances to counteract the harmful effects of others—*i.e.*, on the phenomenon that is usually termed antagonism.

Loew (1899) thought that magnesium poisons the higher plants by displacing the calcium of their nuclei and interfering with the capacity for imbibition belonging to the calcium-protein compounds. An excess of calcium, according to Loew, allows the calcium to enter again into these compounds, and thus counteracts the toxic effect of magnesium. Loew gave this explanation of the often observed antagonistic, or beneficial effect of calcium on plants that have been poisoned by magnesium. The lower plants in Loew's opinion do not have calcium in their nuclei, and hence magnesium does not poison them. Benecke (1907) reported that the toxicity of anions as well as cations for *Spirogyra* could be lessened by the use of calcium. Loew and Aso (1907) thought that potassium salts can retard but not prevent the toxic effects of magnesium salts. They considered that the cause of this retardation of the toxic action by potas-

sium salts is entirely different from the cause underlying the prevention of the toxic action by calcium salts; that it may be due to the formation of double salts with potassium.

Osterhout (1905, 1906, 1907b, 1909) found that fresh water algae were killed by a simple solution of sodium chloride, but that the toxicity of this solution could be inhibited if calcium chloride were added. Studies with marine algae showed that each of the salts of sea water was poisonous in simple solution, but that a mixture of these salts in the proper proportions formed a solution in which the toxic effects of the individual salts were mutually counteracted. This mixed solution was called by Osterhout a "physiologically balanced solution". Some of the salts added to make a solution balanced need not necessarily be nutritive. Thus Osterhout found that sodium and potassium showed great similarity in their toxic and protective or antagonistic effects, but not in their nutritive power. A "nutrient solution" of course contains the salts that are essential for the growth of the plant. If this solution is concentrated, the plants will not thrive in it unless the salts are properly balanced. But a nutrient solution may be made in which the concentrations of the salts are so low as not to exert toxic effects (Osterhout, 1907a).

Lipman (1909, 1910), in testing ammonification by *Bacillus subtilis*, found that there was antagonism between calcium and potassium, magnesium and sodium, and potassium and sodium, but there was none between magnesium and calcium or between sodium and calcium. On the contrary there was a progressive increase in the toxic properties of magnesium and of sodium when calcium was added in increasing amounts to a solution of either one. Loew (1910) thought that this result with magnesium and calcium was to be expected. He states that bacteria in general do not need calcium, and that magnesium in the usual biological concentrations is not toxic to lower fungi and algae; hence these plants do not need any antagonistic element. However, Lipman and Burgess (1914), testing nitrogen fixation, found antagonism between calcium carbonate and magnesium carbonate for *Azotobacter chroococcum*. Greaves (1920) reported antagonism between calcium and magnesium as measured in terms of ammonification and nitrification power of soil. Brooks (1920b), in a study of the respiration of *Bacillus subtilis*, demonstrated marked antagonism between magnesium and sodium chlorides and very slight antagonism between magnesium and calcium chlorides. Other tests by Brooks (1920a) showed a pronounced antagonism between sodium and calcium chlorides.

Winslow and Falk (1923a, 1923b) observed favorable effects with low concentrations of sodium chloride and of calcium chloride, and harmful

effects with large amounts of these salts on *Bacterium coli*. The toxic effect
was greatest with both salts together. Thus their results are in agreement
with those of Lipman with *B. subtilis*.

Lundegardh (1924) reported that *Gibberella Saubinetii* behaves like
the higher plants in showing the antagonistic action of calcium and mag-
nesium. Hawkins (1913) germinated spores of *Glomerella cingulata* in
hanging drops in nutrient solutions. When a salt of zinc, copper, lead, or
aluminum was added, no germination occurred. The addition of calcium
nitrate, magnesium nitrate, or potassium nitrate reduced the toxicity of
all the heavy metals except aluminum.

The effects of antagonistic salts on the respiration of *Aspergillus niger*
were studied by Gustafson (1920). His results with sodium chloride were
contradictory. He believed that this salt has a specific chemical action
which tends to stimulate respiration, while its osmotic pressure tends
to decrease respiration. Sometimes one and sometimes the other effect
prevailed, due to physiological differences in the fungus. He concluded
that low concentrations of sodium chloride and of calcium chloride,
up to 0.5 M, increased respiration, while stronger concentrations decreased
it, due to the osmotic effect. Antagonism was shown by the fact that res-
piration was normal in certain mixtures—that is, it was neither increased
nor decreased. Spores of the fungus did not germinate in 0.5 M sodium
chloride plus dextrose, while they did germinate in the same strength of
calcium chloride plus dextrose, and in various mixtures of the two salts.
This showed, he thought, that a substance may have different effects on
respiration from those which it has on growth.

The present paper deals with some of the problems which have not
been conclusively settled by the work of the authors cited above. It is
concerned with the following problems: (1) the necessity of magnesium
and the toxicity of extremely large amounts of this element for *Aspergillus
niger* and *Penicillium sp.*; (2) the minimum amount of calcium which may
be required by these fungi; (3) the possible antagonistic effects of calcium
toward other metals; and (4) improvements in the proportions of the salts
used in the three-salt solution of Pfeffer. After a description has been
given of the general methods that were employed, the experiments and
results will be discussed under the four topics just indicated.

METHODS

This work was begun in the botanical laboratory of Barnard College
under the direction of the late Prof. Herbert M. Richards. It was con-
tinued and finished in the laboratory of plant physiology at Columbia
University under the guidance of Professor Sam F. Trelease, to whom the

writer wishes to express her gratitude for his interest and many helpful suggestions. The *Aspergillus* used in performing the series of experiments described in the ensuing pages is believed to be the same organism which was brought from Pfeffer's laboratory in Leipzig by Professor Richards about thirty-five years ago. Dr. Charles Thom, of the United States Department of Agriculture, to whom a culture of the organism was recently sent for examination, decided that it should be regarded as a morphologically aberrant strain of *A. niger*, which may best be designated as "Richards' strain." A descriptive note kindly supplied by Doctor Thom follows:

> *Aspergillus niger* (Richards' strain). This strain varies from the usual races or strains of *A. niger* in the thin-walled stalks, more than usually stained with aspergillin, vesicles quite brittle, primary sterigmata shorter during the usual growing period, but becoming longer in individual heads in old culture. The measurements found when young were near those given by Amons (Thom and Church, 1926, p. 174) for his strain labelled *A. ficuum*, but there is no way of proving identity. Further, there does not appear to be ground for believing that the name *A. ficuum* belonged to Amons' strain since the organism distributed from Berlin and by Dr. Westerdijk from the "Central-bureau" at Baarn was certainly not this one. Until more comparative studies are made, the separation of varieties or species among these black forms is scarcely profitable.

A few experiments were also performed with a strain of *Penicillium* isolated from the air, stock cultures of which were maintained on malt-agar slants. The stock cultures of the *Aspergillus* were grown an slices of bread in deep Petri dishes.

The basic nutrient solution used was Pfeffer's three-salt solution with sucrose as the source of carbon. No iron, zinc, copper, or manganese was added. If these elements are needed, they were probably furnished in sufficient amounts by impurities in the salts.

Pfeffer's solution

	Grams per liter	Gram-molecules per liter
Sucrose ($C_{12}H_{22}O_{11}$)	50.0	0.14612
Ammonium nitrate (NH_4NO_3)	10.0	0.12492
Monopotassium phosphate (KH_2PO_4)	5.0	0.03673
Magnesium sulphate ($MgSO_4 \cdot 7H_2O$)	2.5	0.01014
Total salt concentration	17.5	0.17179

The sucrose and salts were obtained from different sources during the six years in which the experiments were carried on. Their purity sometimes varied. This might not have been noticed in dealing with higher plants, but *Aspergillus* has been found to be extraordinarily sensitive to certain minute differences in the medium. The presence of certain kinds of im-

purities could be detected by the fact that the control culture was slightly stimulated—that is, the mycelial felts were wrinkled and abnormally heavy, and spore production was diminished. If this occurred, salts from other sources were tried, until the control culture gave a normal result— that is, a flat, black, evenly fruited felt, having a weight of approximately 0.30 gram.

A determination of the hydrogen-ion concentration of the culture solution proved to be useful, in conjunction with the appearance of the felts, as a guide in deciding whether the control culture was normal. The pH value of the solution, after normal growth of the fungus, was 2.8 with metacresol purple and 3.0 with bromphenol blue, using the La Motte standard indicator solutions. An aberrant pH value was indicative of abnormal growth. Stimulation—and sometimes inhibition—of growth could be detected by a lowering of the pH value to 1.8. Decreased growth sometimes was associated with a pH value of 3.2 or 3.4. The pH value of the basic solution was always determined before growing the fungus. It was invariably 4.4.

The water used for the final rinsing of glassware and for making solutions was obtained from a Barnstead still and redistilled through a quartz condenser. It was stored in Pyrex flasks. All glassware was treated with concentrated sulphuric acid, and then thoroughly rinsed with tapwater, with single-distilled water and finally with double-distilled water.

The stock solutions of the salts were made up in the desired concentrations and stored in Pyrex bottles, while the sugar solution was made fresh each time of using. The culture solutions were prepared before each experiment by mixing and diluting the stock solutions, to give the required molar concentrations in the final solution.

The fungus was grown in 150 cc. Pyrex flasks of Erlenmeyer form, stoppered with cotton plugs, on 50 cc. of culture solution. The flasks and solutions were sterilized once, for 30 minutes, in an Arnold steam-sterilizer. The inoculations of the solutions in the flasks were made from the stock culture on bread by means of a platinum loop. Care was taken to avoid inclusion of mycelium with the spores. It was possible to cover the surface of the liquid in each flask completely and uniformly with spores; but of course the number of spores placed in each flask must have varied somewhat. That irregularities in the sowing make no important difference in the weights of the felts, after several days' growth, was shown by Linossier (1919), working with Oïdium lactis, and the general uniformity of the dry weights of duplicated cultures in the present experiments showed that serious errors were not introduced by irregularities in inoculation.

After the Aspergillus cultures had grown for five days in an incubator

at 34°C., the mycelial felts were placed on weighed filter papers, washed twice with distilled water, dried for three days at 65°C., put into a desiccator, and then weighed. From the total weight was subtracted the weight of the filter paper previously taken, thus giving the weight of the felt. Before the filter papers were weighed, they were dried at 65°C. and placed in a desiccator, so that they were in the same condition as when they were weighed the second time, with the fungus felts. The *Penicillium* cultures were grown for six days at room temperature (about 22°C.). In all other respects they were treated in the same way as the *Aspergillus* cultures.

RESULTS AND DISCUSSION

Necessity of magnesium

Benecke, Molisch, Günther, Javillier and Canals, as mentioned in the introduction to this paper, have all concluded from their investigations that magnesium is essential for the development of *Aspergillus niger*. Nevertheless, it seemed desirable in the present study to make further tests of the influence of magnesium sulphate and of magnesium upon the growth of this fungus as well as upon the growth of a species of *Penicillium*. Two series of experiments were carried out. In the first series, magnesium sulphate was omitted from one culture solution and was added in increasing concentrations to the others. The results are given in table 1 and are plotted as graphs in figure 1.

The *Aspergillus* and the *Penicillium* made practically no growth when magnesium sulphate was absent from the nutrient solution. Only a few

TABLE 1

Growth of Aspergillus niger and Penicillium sp. as related to the concentration of magnesium sulphate in Pfeffer's solution. No magnesium sulphate in basic solution.

CONCENTRATION OF MgSO$_4$	DRY WEIGHT OF MYCELIUM[a]	
	Aspergillus niger	Penicillium sp.
M	*Grams*	*Grams*
Zero	.024	.008
.0000208	.104	.044
.000125	.251	.132
.00025	.278	.143
.0005	.305	.143
.00125	.303	.150
.0025	.322	.152
.005	.328	.149
.01	.333[b]	.154[b]
.02	.379	.162

[a] Each value represents the mean for 10 cultures.
[b] Control culture, supplied with same concentration as in Pfeffer's solution.

scattered white patches of very thin mycelium developed on the surface of the medium from which magnesium sulphate had been omitted; germination of the spores began, but growth ceased after a short time.

That the increase in weight of the felts of both fungi varies directly as the increase in concentration of magnesium sulphate, up to at least twice the concentration of this salt in Pfeffer's solution, may be seen by referring to the graphs of figure 1. Both of the curves ascend steadily up to the point denoting the highest concentration used in this series. This was 0.02 M magnesium sulphate—double the concentration of this salt in Pfeffer's solution. As would be expected, both curves rise more rapidly in the
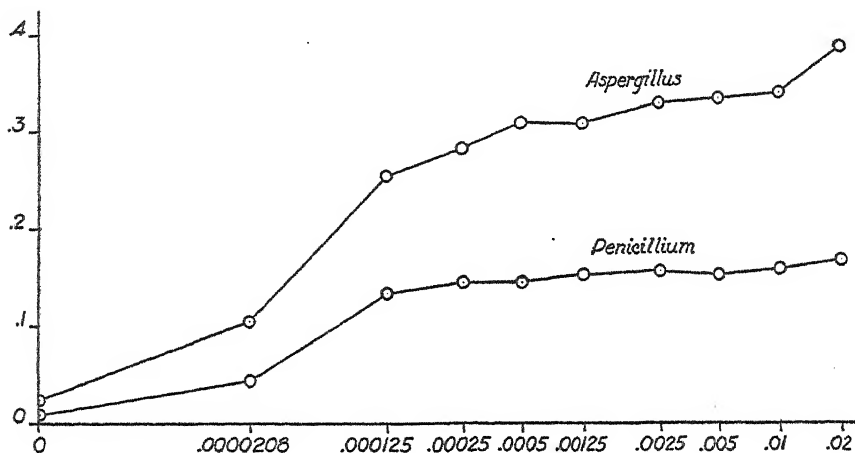
Fig. 1. Dry weights of felts of *Aspergillus niger* and *Penicillium sp.* as related to the concentration of magnesium sulphate in Pfeffer's solution. Magnesium sulphate omitted from basic solution. Abscissas represent molar concentrations of magnesium sulphate (logarithmic scale). Ordinates represent weights of felts in grams. Control culture, supplied with same concentration (0.01 M) magnesium sulphate as in Pfeffer's solution, gave yields of 0.333 gram for *Aspergillus*, and 0.154 gram for *Penicillium*.

lower portion of the concentration range than in the higher. This feature would of course be much more prominent in graphs plotted on an ordinary scale of abscissas than it is in figure 1 in which concentrations are plotted on a logarithmic scale. The results secured in this test are similar to those of Benecke (1896), who obtained higher dry weights of felts of *Aspergillus niger* by increasing the concentration of magnesium sulphate in the nutrient solution.

In the second series of experiments the influence of various concentrations of the magnesium ion was tested by adding magnesium sulphate to a basic solution to which the sulphate ion had been supplied as potassium sulphate. The solution which lacked only the magnesium gave no growth

of *Aspergillus niger*. The results of adding various amounts of magnesium, by means of the same concentrations of magnesium sulphate used in the last experiment, are shown in table 2, and are plotted as a graph in figure 2. It will be noticed that the curves for *Aspergillus* in figures 1 and 2 follow practically the same course. The addition of magnesium sulphate to this solution gave almost the same result as it gave in the first series of ex-

TABLE 2

Growth of Aspergillus niger as related to the concentration of the magnesium ion in Pfeffer's solution. Magnesium sulphate of the basic solution replaced by potassium sulphate.

CONCENTRATION OF MgSO₄	DRY WEIGHT OF MYCELIUM[a]
M	*Grams*
Zero	.005
.0000208	.161
.000125	.276
.00025	.274
.0005	.297
.00125	.276
.0025	.288
.005	.312
.01	.336[b]
.02	.362

[a] Each value represents the mean for 5 cultures.
[b] Control culture, supplied with same concentration as in Pfeffer's solution.
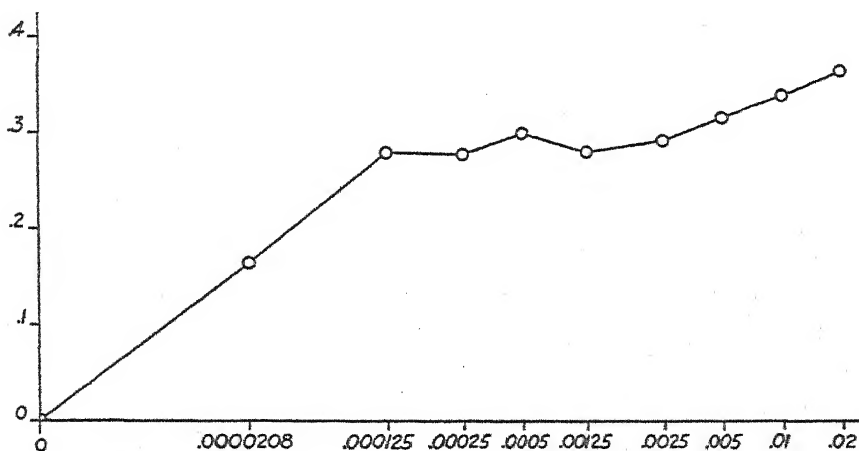
Fig. 2. Dry weights of felts of *Aspergillus niger* as related to the concentration of the magnesium ion in Pfeffer's solution. Magnesium sulphate of basic solution replaced by potassium sulphate. Abscissas represent molar concentrations of magnesium sulphate (logarithmic scale). Ordinates represent weights of felts in grams. Control culture, supplied with same concentration (0.01 M) magnesium sulphate as in Pfeffer's solution (in addition to potassium sulphate) gave yield of 0.336 gram.

periments, in which no potassium sulphate was used in the basic solution. There is a gradually increasing weight of felts as more and more of the magnesium ion is added. It will be observed that in the lower concentrations the curve of figure 1 rises with a slightly steeper slope than that of figure 2. This difference may be attributed to the fact that in the first series both the sulphate ion and the magnesium ion were absent from the basic solution, whereas in the second series only the magnesium ion was omitted from the basic solution.

The close similarity between the parts of the curves corresponding to concentrations of magnesium sulphate greater than 0.00025 M indicates that the higher concentrations of the sulphate ion had little or no influence on the growth of *Aspergillus*.

The second series of experiments was performed only with *Aspergillus niger*, but four cultures of each of the two fungi gave no growth with ammonium sulphate in place of magnesium sulphate. It is therefore clear that the magnesium ion is essential for the growth of both *Aspergillus* and *Penicillium*.

The minimum amount of calcium which may be necessary

Most authors have considered that calcium is unnecessary for the growth of fungi. Benecke, Molisch, Wehmer, Loew, Buromsky, Winogradsky, Steinberg, Dunn, and Lundegardh, as quoted above, have all come to this conclusion. On the other hand, the experiments of Haenseler, Young and Bennett, Coupin, Davis, Marloth and Bishop, Hori, Gabritschewsky, and O. Richards, also cited in the introduction to this paper, have shown some favorable results from its use.

The experiments described in this section of the present paper were planned to throw some light on the question of the minimum amount of calcium which may be necessary for the growth of *Aspergillus*. The tests were of several different types, each of which gave some information concerning this problem.

In one set of tests special precautions were taken to make sure that no calcium was added to the nutrient solution by the water or glassware. Accordingly, the usual procedure was somewhat modified. The double distilled water was redistilled through the same quartz condenser, and collected in quartz flasks. The sugar used was of special purity—Kahlbaum "precip. for calorimetric analysis". The salts and sugar were weighed and dissolved directly in the distilled water contained in a large quartz beaker, and the solution was sterilized by being brought to the boiling point in this beaker. Smaller quartz beakers were used for the culture of the fungi, and quartz pipettes were employed in measuring the water and

solution. Therefore, the only sources of calcium which remained were the salts or the fungus spores.

The weights of the fungus felts of *Aspergillus* and *Penicillium* which were grown in this solution are given in table 3. It will be seen that they are essentially the same as those obtained when these fungi were grown under similar conditions, altered only by the addition of 0.00008 M and 0.001 M calcium nitrate. Moreover, the power of conidium formation was not noticeably modified in either fungus by the addition of these amounts of calcium nitrate.

It is realized of course that this test is not in itself very conclusive, since the salts and the fungus spores probably contained some calcium—more, in fact, than would be derived from the water or glassware. The

TABLE 3

Growth of Aspergillus niger and Penicillium sp. in Pfeffer's solution to which calcium nitrate has been added.

CONCENTRATION OF Ca(NO₃)₂	DRY WEIGHT OF MYCELIUM[a]	
	Aspergillus niger	Penicillium sp.
M	Grams	Grams
Zero	.291[b]	.213[b]
.00008	.287	.194
.001	.302	.185

[a] Each value represents the mean for 20 cultures of *Aspergillus niger* or for 16 cultures of *Penicillium sp.*

[b] Control culture.

salts, however, were of best obtainable reagent or chemically pure grades, and their printed analyses showed only very small quantities of calcium. And the test may be considered to indicate that the amount of calcium required—if any—is exceedingly small in comparison with the quantities of the other elements needed for the growth of these fungi. It will be recalled that Benecke (1894a) obtained no increase of growth by adding calcium sulphate to his solution which already contained magnesium sulphate.

Another test was made in which calcium chloride was added to Pfeffer's solution. The results, shown in figure 6 plotted from the data of table 7, show that the addition of this calcium salt in various concentrations had no appreciable effect on the dry yields of *Aspergillus*. Thus it seems clear that the presence of significantly large amounts of calcium, as the nitrate, sulphate, or chloride, in Pfeffer's solution has no beneficial influence on the growth of *Aspergillus* or *Penicillium*.

In an attempt to obtain further evidence regarding the possibility that calcium might be beneficial to *Aspergillus*, a series of experiments was con-

does the calcium nitrate curve lie near that for ammonium nitrate. At one of these, representing a molar concentration of 0.05, the calcium nitrate curve is slightly above that of ammonium nitrate; and at the next point, 0.124 M, it is nearly as high as the curve for ammonium nitrate. In addition to being heavier, the felts of the ammonium nitrate series had a much healthier appearance, as far as amount and blackness of the conidia were concerned, than had those grown with the other three nitrates. This was true at all tested concentrations.

At the highest concentrations of ammonium nitrate used—*i.e.*, 0.2 and 0.4 M—the fungus made very good growth, giving dry weights of 0.310 and 0.371 gram, respectively. In other experiments during the course of this work, the dry yields obtained with 0.124 M ammonium nitrate (the standard concentration in Pfeffer's solution) often nearly approached these weights. This may be seen by referring to the controls in the potassium and sodium series of table 4, and the controls in tables 1, 2, 6, and 13. It does not seem, therefore, that 0.2 M and 0.4 M ammonium nitrate have acted as a "stimulant" to the growth of *Aspergillus*, if the growth in Pfeffer's solution may be taken as normal. The growth in this solution was found to vary from 0.245 to 0.370 gram dry weight. Buromsky (1913) thought that ammonium nitrate could be compared to zinc sulphate as a stimulant, because ammonium nitrate gave a higher respiration coefficient than ammonium sulphate when used in his nutrient solution. He found that when zinc sulphate was added to the solution containing ammonium sulphate, the coefficient of respiration was raised to almost equal that obtained with ammonium nitrate alone.

On the whole, it may be concluded that calcium nitrate was not very satisfactory as a mineral nutrient for *Aspergillus niger* in this series of experiments, although it gave greater mycelial weights than potassium nitrate, as in the work of Young and Bennett (1922), and greater than sodium nitrate, as in the study by Haenseler (1921). Calcium in no way made up for the absence of ammonium nitrogen, which many workers have reported as the most favorable source of nitrogen for the growth of *Aspergillus*. Boas (1919) and Boas and Leberle (1919) found that an ammonium salt, especially the chloride, was used by *Aspergillus* to a much greater extent than more highly organized nitrogenous compounds offered at the same time. They considered that the ease of dissociation and of entrance into the cell determined the choice of a source of nitrogen by the fungus. Brenner (1914), having tried many sources of nitrogen, concluded that ammonium salts and asparagin gave the best growth of *Aspergillus*.

The experiments described thus far have shown that calcium is not required in any considerable amount by *Aspergillus*, and that relatively high

concentrations of a salt of this element have detrimental, rather than beneficial, effects upon the growth of this organism. There still remains the possibility that very small quantities of calcium are essential for *Aspergillus*. Definite proof that calcium is indispensable could of course be obtained if the calcium content of the culture medium could be sufficiently reduced to prevent the growth of the fungus. In a similar manner, for example, conclusive evidence has been presented during the last decade that small quantities of zinc, manganese, boron, copper, etc., are essential for the growth of many of the higher green plants. It seemed worth while in the present study to reduce the calcium content of the nutrient solution to a very low minimum and to see whether this solution would allow the development of *Aspergillus*. A culture medium of very low calcium content was prepared by adding sodium oxalate to Pfeffer's solution, in concentrations sufficiently high to precipitate practically all of the calcium that might be present as an impurity. The preparation of the culture solution was thus essentially the same as that recommended by Loew (1892, 1898, 1899, 1925), Hori (1910), and Pringsheim (1926).

A test was made of the ability of *Aspergillus* to grow in Pfeffer's solution to which had been added sodium oxalate in the five following concentrations: 0.00625 M, 0.0125 M, 0.025 M, 0.05 M, and 0.1 M. A rather surprising result was obtained, as may be seen from the graph of figure 4, plotted from the data of table 5. The growth of the fungus was greatly

TABLE 5

Growth of Aspergillus niger in Pfeffer's solution containing sodium oxalate.

CONCENTRATION OF $Na_2C_2O_4$	DRY WEIGHT OF MYCELIUM[a]
M	*Grams*
Zero	.284[b]
.00625	.346
.0125	.351
.025	.384
.05	.472
.1	.583

[a] Each value represents the mean for 9 cultures.
[b] Control culture, represents the mean for 18 cultures.

improved by the addition of all tested concentrations of oxalate. The highest concentration used gave very heavy felts. This increased growth may have been due to a stimulating effect of some impurity in the sodium oxalate or to the ability of the fungus to make use of the carbon of sodium oxalate. Since the fruiting was excellent, while fruiting would be inhibited by the typical zinc sulphate stimulation, it seems probable that the greatly

increased weights may have been due to the addition of a second source of carbon for the fungus.

A test was made to find out approximately how much calcium might have been present as an impurity in the nutrient solution employed in the experiment just described. A series of five solutions, having the same composition as those used in the growth test, were freshly prepared. Thus they contained the components of Pfeffer's solution with the addition of
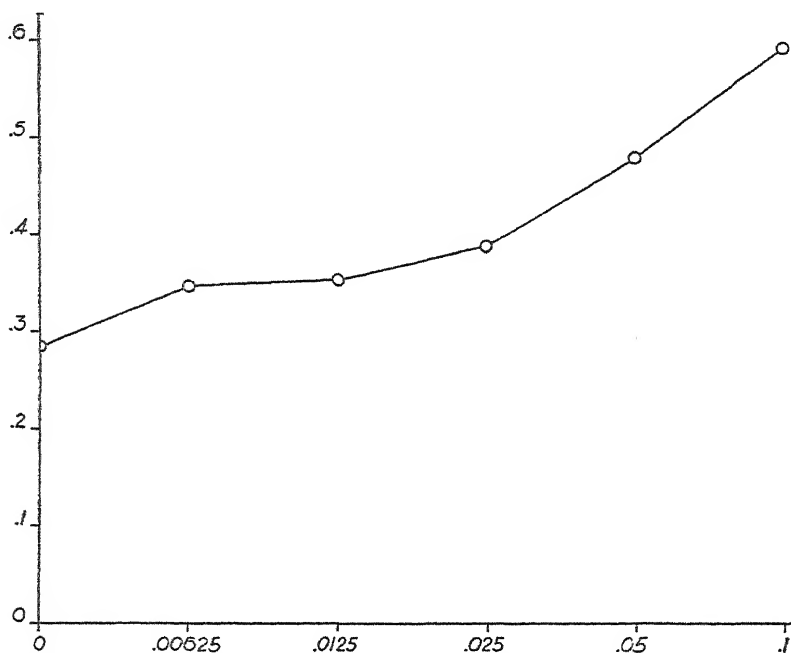
Fig. 4. Dry weights of felts of *Aspergillus niger* grown in Pfeffer's solution to which sodium oxalate was added. Abscissas represent molar concentrations of sodium oxalate (logarithmic scale). Ordinates represent weights of felts in grams. Control culture without sodium oxalate gave yield of 0.284 gram.

0.00625 M, 0.0125 M, 0.025 M, 0.05 M, and 0.1 M sodium oxalate, respectively. Each of these solutions was then tested by adding separately five different concentrations of calcium chloride. The concentrations of this salt employed were 0.0000001 M, 0.000001 M, 0.00001 M, 0.0001 M, and 0.001 M, respectively. This gave a series of twenty-five tests. It was found that the three strongest calcium chloride concentrations (0.00001 M, 0.0001 M, 0.001 M) gave precipitates of calcium oxalate with all of the five oxalate concentrations (0.00625 M, 0.0125 M, 0.025 M, 0.05 M, 0.1 M), and that 0.000001 M calcium chloride gave a visible precipitate with 0.1 M sodium oxalate, but not with the concentrations of oxalate below

this. The lowest concentration of calcium chloride (0.0000001 M) gave no visible precipitate with any of the sodium oxalate concentrations used.

After the fungus had been grown in the same concentrations of sodium oxalate added to Pfeffer's solution, the felts were removed and each of the five culture solutions was tested again, by means of the same five concentrations of calcium chloride. The results were the same as those obtained with the original culture solutions that had been supplied to the fungus. The 0.000001 M calcium chloride solution again gave a precipitate with 0.1 M oxalate.

These tests indicate that, had there been a calcium salt present in a strength of 0.000001 M in the nutrient solution in which *Aspergillus niger* was grown, a precipitation of calcium oxalate would have been observed, since sodium oxalate was present in this nutrient solution in a concentration of 0.1 M. As just pointed out, a precipitate was clearly perceptible when 0.000001 M calcium chloride was added to the solution containing 0.1 M sodium oxalate, both before and after growing the fungus, and no such precipitate was observed in the solution until the addition of calcium chloride. This experiment seems to show definitely that probably less than 0.000001 M of calcium impurities was present in a solution that gave excellent growth of *Aspergillus niger*. This would represent less than 1 part of calcium per 25 million of culture solution. From these tests it may be concluded that, if calcium is indispensable for the growth of *Aspergillus*, the quantity required would be no greater than the amounts of boron, manganese, zinc, and copper that have been found to be essential for many of the higher green plants.

An interesting comparison may be made between the results obtained with *Aspergillus* and those reported by Pringsheim (1926) for various kinds of algae. In one set of experiments Pringsheim first tested numerous algae by the use of solutions as free from calcium as he could make them. He divided these algae into three groups: those which gave no growth without calcium; those for which the deficiency of calcium made little noticeable difference; and those which showed poorer growth but did show some growth without calcium. He then experimented upon the growth of these organisms in a nutrient solution containing sodium oxalate. The culture solution was tested for calcium precipitation, before and after the organisms had grown in it, by the addition of 1 cc. of 0.1 per cent calcium chloride solution. Pringsheim thought, because of the precipitate which he obtained with this concentration of calcium chloride, that a sufficient amount of sodium oxalate was in the nutrient solution to have precipitated calcium from the algal cell had it been present there. The algae which seemed to require calcium in his first experiments did not

grow in the solution containing sodium oxalate. The algae which did not seem to require calcium in his first experiments grew well in the oxalate solutions. There were a few exceptions in which algae which had seemed to need calcium in the first experiments gave favorable results with the oxalate solutions. He accounted for this by saying that their calcium requirements were unusually low, and that enough calcium might have remained in the solution to satisfy these requirements, in spite of the presence of oxalates.

The method of spectrographic analysis furnishes a much more delicate test for calcium than could be obtained by the precipitation method described in the foregoing paragraphs. The chemical precipitation method was only delicate enough to indicate that the culture solution contained less than 0.000001 M calcium. The concentration of calcium in the presence of 0.1 M sodium oxalate may actually have been much smaller than 0.000001 M. It would have been desirable to have had a spectrographic test made upon the mycelium of *Aspergillus* that had been grown in the culture solution containing a high concentration of sodium oxalate, as well as upon a filtered sample of the culture solution itself. But it was not feasible at the time to have this done. One spectrographic analysis, however, was made in the present study, and this was made under control conditions; the fungus was grown in Pfeffer's solution to which no oxalate had been added. This test was made through the courtesy and cooperation of Dr. Andrew Dingwall, of the Department of Chemistry of Columbia University, upon ash obtained from three flat black felts grown in a solution to which no calcium was consciously added in any way. The water was doubly distilled through quartz condensers and the salts were the purest obtainable. The felts, before ashing, were washed many times, using two liters of double distilled water, to remove traces of the culture medium. The ash was found to contain considerable quantities of magnesium and potassium, as might have been expected. In addition there were found small amounts of calcium, iron, manganese, lead, aluminum, and sodium. Other elements may have been present, but a search was not made for them.

The fungus felts may have held these substances in two ways: (1) as materials retained between the hyphal threads by occlusion, (2) as actual components of the fungus cells. Considering the compactness and smoothness of the felts, it seems unlikely that significant quantities of the medium were occluded. The fungus itself probably contained these minute quantities of various elements. They may have been obtained from the bread on which the stock cultures were grown and stored in the spores. Aso (1900) found calcium among the minerals of the ash from the spores of *Aspergillus*

oryzae. Or these elements may have been secured by absorption from impurities in the salts dissolved in the liquid medium. It is of course known that many plants absorb and accumulate substances that are present in extremely low concentrations in the medium in which the plants live. A striking example is furnished by the accumulation of iodine in the giant kelps of the Pacific Ocean.

Effect of calcium chloride in solutions containing certain other salts

That the toxic effect of one cation may be more or less neutralized by the antitoxic effect of another, when they are supplied together in a culture solution for plants, has been observed by many investigators. Some of the pioneer work in this field has been carried on by Loew and Osterhout, as discussed in the introduction to this paper. Mention may be made here of the more recent work of Trelease and Trelease (1926) and Eisenmenger (1928), who conducted experiments which showed that wheat roots are poisoned by relatively high concentrations of a magnesium salt, when grown in a solution of this salt alone. Their results showed that this toxicity may be counteracted by the addition of a calcium salt. A clear demonstration of antagonistic action is obtained most readily with very simple solutions, containing only two salts. In a culture solution containing several salts, the antagonistic relations are very complicated, owing to the chance for the mutual interaction of a large number of ions. But in some cases the antitoxic action of calcium is so pronounced that it can be easily demonstrated with the mixed solutions used for growing the higher plants. Thus, magnesium injury of wheat has been shown to depend upon the ratio of calcium to magnesium in the culture solution (Trelease and Trelease, 1931.)

A series of experiments was carried out with *Aspergillus niger* to see whether calcium, when added to Pfeffer's solution, would have an an-

TABLE 6

Growth of Aspergillus niger in Pfeffer's solution containing magnesium chloride.

CONCENTRATION OF MgCl$_2$	DRY WEIGHT OF MYCELIUM[a]
M	*Grams*
Zero	.339[b]
.2	.331
.4	.334
.6	.236
.8	.223
1.2	.130
1.6	.129

[a] Each value represents the mean for 6 cultures.
[b] Control culture.

tagonistic effect toward other substances present in the culture solution. One set of tests was planned to determine whether magnesium chloride would be toxic for *Aspergillus* when used in high concentrations in the solution; and if so, whether the addition of a calcium salt would counteract the toxicity.

Magnesium chloride was added to Pfeffer's solution in concentrations varying from 0.2 M to 1.6 M. The results of this experiment may be seen by referring to the graph of figure 5, plotted from the data given in table 6. It will be noted that the two lowest concentrations used—namely, 0.2 M and 0.4 M—had very little effect on the growth of the fungus. The weight was normal and there was slight fruiting. At concentrations of 0.6 M and
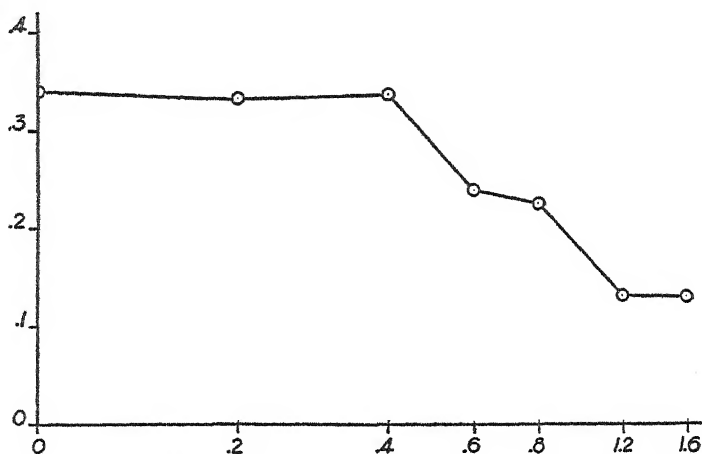
Fig. 5. Dry weights of felts of *Aspergillus niger* grown in Pfeffer's solution to which magnesium chloride was added. Abscissas represent molar concentrations of magnesium chloride (logarithmic scale). Ordinates represent weights of felts in grams. Control culture without magnesium chloride gave yield of 0.339 gram.

upwards, the growth of the fungus was inhibited. The dry weights were consistently reduced, until at 1.2 M and 1.6 M magnesium chloride they were only 38 per cent of the control dry weight of 0.339 gram. The appearance of these last felts was very far from normal. They were white and lacy and completely lacking in conidia.

It is therefore clear that magnesium chloride, if supplied in very high concentrations, inhibits the growth of *Aspergillus niger*. This corresponds to the action of high concentrations of magnesium salts on wheat roots, mentioned above. The concentration of the magnesium ion, however, which is necessary to check the growth of the fungus (0.6 M) is actually considerably higher than necessary to show a similar effect on wheat roots.

Magnesium sulphate is definitely toxic to wheat roots at a concentration of 0.001 M, according to Eisenmenger (1928).

Before testing the effect of the magnesium and calcium chlorides together, the latter was added alone to Pfeffer's solution in concentrations ranging from 0.00625 M to 0.1 M. The graph of figure 6, plotted from the

TABLE 7

Growth of Aspergillus niger in Pfeffer's solution containing calcium chloride.

CONCENTRATION OF CaCl₂	DRY WEIGHT OF MYCELIUM[a]
M	*Grams*
Zero	.261[b]
.00625	.266
.0125	.284
.025	.272
.05	.282
.1	.265

[a] Each value represents the mean for 9 cultures.
[b] Control culture.

data given in table 7, shows an almost straight, horizontal line. The sporulation of the felts was good at all concentrations. Hence calcium chloride had no effect on the dry weight or fruiting of *Aspergillus niger* at any concentration used.
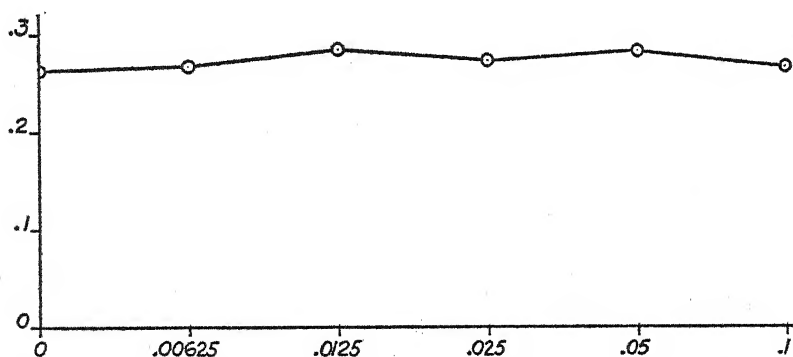
Fig. 6. Dry weights of felts of *Aspergillus niger* grown in Pfeffer's solution to which calcium chloride was added. Abscissas represent molar concentrations of calcium chloride (logarithmic scale). Ordinates represent weights of felts in grams. Control culture without calcium chloride gave yield of 0.261 gram.

Since a concentration of 0.8 M magnesium chloride had been found to inhibit the growth of *Aspergillus* very considerably, this concentration was chosen for use in Pfeffer's solution with various concentrations of calcium chloride. The results of this experiment are shown on the graph

of figure 7, plotted from the data of table 8. It may be seen here that the toxic effect of the magnesium chloride was as great as in the previous test. As the concentration of calcium chloride increases from 0.0001 M to 0.01

TABLE 8

Growth of Aspergillus niger in Pfeffer's solution containing calcium chloride and magnesium chloride.

CONCENTRATIONS		DRY WEIGHT OF MYCELIUM[a]
MgCl₂	CaCl₂	

$MgCl_2$	$CaCl_2$	DRY WEIGHT OF MYCELIUM[a]
M	*M*	*Grams*
Zero	Zero	.297[b]
.8	Zero	.223
.8	.0001	.226
.8	.001	.241
.8	.01	.234
.8	.1	.193

[a] Each value represents the mean for 12 cultures.
[b] Control culture.

M the graph continues practically parallel with the base line. At a concentration of 0.1 M calcium chloride with 0.8 M magnesium chloride, the dry weight was even somewhat lowered. The graph appears to show no significant rise, as it would have shown had there been antagonism. The
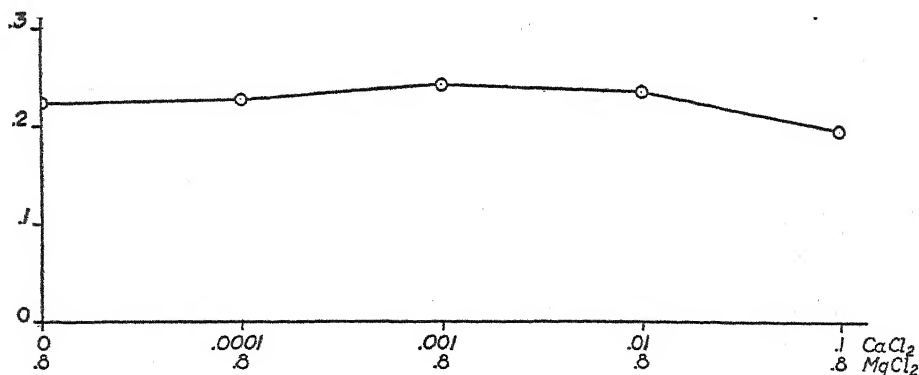
Fig. 7. Dry weights of felts of *Aspergillus niger* grown in Pfeffer's solution containing calcium chloride and magnesium chloride. Each culture contained 0.8 M magnesium chloride. Abscissas represent molar concentrations of calcium chloride (logarithmic scale). Ordinates represent weights of felts in grams. Control culture without magnesium or calcium chlorides gave yield of 0.297 gram.

weights of the felts are all essentially the same as those obtained with 0.8 M magnesium chloride without the addition of any calcium chloride. All of the felts grown in solutions containing both calcium and magnesium chlorides were white, and they were completely lacking in conidia. They

were similar in appearance to those obtained in Pfeffer's solution to which magnesium chloride alone was added. From this experiment it may be seen that the addition of calcium chloride helped neither the growth nor the sporulation of *Aspergillus*, when these were inhibited by a high concentration of magnesium chloride in the culture solution.

Calcium chloride, therefore, seems to have no antitoxic action for magnesium chloride under the conditions of the present tests with *Aspergillus niger*. This lack of antagonism agrees with Lipman's results for *Bacillus subtilis*, previously discussed. But the toxicity of magnesium chloride for *Aspergillus niger* was not increased by calcium chloride (except possibly at a concentration of 0.1 M), as Lipman found to be the case with *Bacillus subtilis*. Loew (1892) stated that magnesium salts in the absence of calcium salts are not harmful to the fungi; he probably referred to low concentrations, as he says later (1910) that they are not harmful in the usual biological concentrations, and that hence there is no need of an antagonistic element. It was only possible to obtain a toxic effect on *Aspergillus* by using concentrations of magnesium chloride which are far higher than those used in most nutrient solutions. Thus, the harmful effect may have been due to the high osmotic concentration of the salt used (0.8 M). Against this view, however, is the stimulation of growth observed with 0.8 M sodium chloride (figure 8), having an osmotic value about two-thirds as great as that of the magnesium chloride. That antagonism between calcium and magnesium does exist for some of the lower organisms has been shown by the work of Lipman and Burgess (1914), Greaves (1920), Brooks (1920a, 1920b), and Lundegardh (1924), cited above.

The possibility of an antagonistic action between sodium and calcium was next considered. To observe the effect of sodium chloride on *Aspergillus niger*, this salt was added to Pfeffer's solution in concentrations varying from 0.1 M to 0.8 M. The results of this experiment may be seen by referring to the graph of figure 8, plotted from the data given in table 9.

TABLE 9

Growth of Aspergillus niger in Pfeffer's solution containing sodium chloride.

CONCENTRATION OF NaCl	DRY WEIGHT OF MYCELIUM[a]
M	*Grams*
Zero	.245[b]
.1	.352
.2	.414
.3	.408
.4	.407
.8	.436

[a] Each value represents the mean for 10 cultures.
[b] Control culture.

It will be noted that sodium chloride, at all tested concentrations, stimulated the growth of the fungus, as indicated by dry weight of mycelium. With increasing concentrations of sodium chloride, the growth curve rises rapidly at first and then more slowly. Although the dry yields are nearly the same throughout a considerable range of concentrations, the greatest dry weight is indicated for the highest tested concentration of sodium chloride—namely, 0.8 M. It is rather surprising that the fungus grew so well in Pfeffer's solution containing such a high concentration of sodium chloride. Spore formation was almost normal at a concentration of 0.1 M
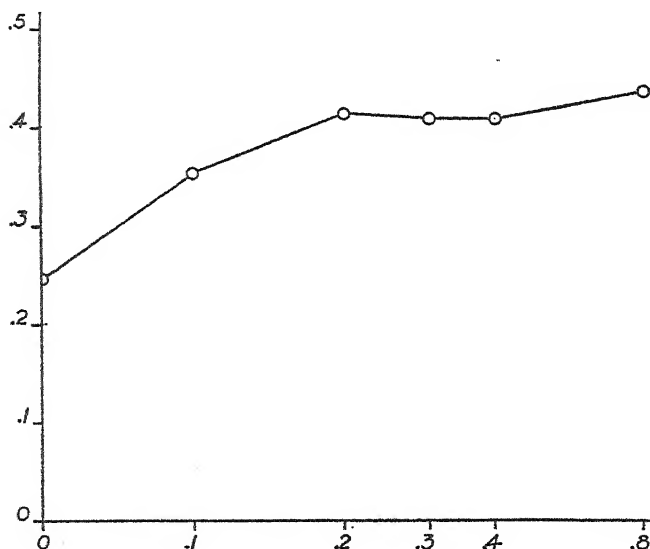
Fig. 8. Dry weights of felts of *Aspergillus niger* grown in Pfeffer's solution to which sodium chloride was added. Abscissas represent molar concentrations of sodium chloride (logarithmic scale). Ordinates represent weights of felts in grams. Control culture without sodium chloride gave yield of 0.245 gram.

sodium chloride and decreased gradually with increasing concentration of the salt, until at 0.4 M the spores were very few in number. There were almost no spores produced at the highest concentration—0.8 M. These results agree in general with those obtained by Molliard (1921), who found that the growth of *Sterigmatocystis nigra* was normal when he added sodium chloride in concentrations of 0.04 M to 0.13 M to a nutrient solution. Few conidia were formed at 0.17 M and none at 0.51 M. The rate of growth diminished as the concentration increased from 0.34 M to 0.86 M; growth was very slow at 1.71 M and was entirely inhibited at 2.05 M. It will be noted, however, that mycelial growth was stimulated in the present tests by concentrations which Molliard found to be toxic.

For studying the combined effects of sodium chloride and calcium chloride in Pfeffer's solution, a series of solutions was employed in which the concentration of sodium chloride was kept uniform, at 0.8 M; this concentration, as just shown, had a marked stimulating effect on mycelial growth. To these solutions, calcium chloride was added in concentrations ranging from zero to 0.1 M.

The results of this experiment may be seen by referring to the graph of figure 9, plotted from the data of table 10. It will be observed that the

TABLE 10

Influence of calcium chloride upon the growth of Aspergillus niger in Pfeffer's solution containing a stimulating concentration of sodium chloride.

CONCENTRATIONS		DRY WEIGHT OF MYCELIUM[a]
NaCl	CaCl$_2$	
M	*M*	*Grams*
Zero	Zero	.292[b]
.8	Zero	.436
.8	.0001	.403
.8	.001	.390
.8	.01	.360
.8	.1	.243

[a] Each value represents the mean for 8 cultures.
[b] Control culture.

curve representing the dry weights of fungus felts drops gradually as the concentration of calcium chloride in the mixed solution increases. Thus, the stimulating effect of sodium chloride on mycelial growth is gradually diminished when calcium chloride is added in increasing concentrations to the solution. A rather abrupt drop in the curve brings the dry weight for the mixture containing 0.1 M calcium chloride to a lower value than that for the control culture (table 10); stimulation has been completely inhibited and this mixture is actually toxic for mycelial growth.

Fruiting of the fungus in the solutions containing calcium chloride and sodium chloride was even less abundant than in the solution to which sodium chloride alone had been added. Conidium formation was completely inhibited in the mixed solution containing 0.1 M calcium chloride.

The question may be raised as to whether the term antagonism should be applied to the effect of one salt in diminishing the stimulation due to another. This term has usually been used with reference to a decrease in toxic action. Calcium chloride, as noted above, reduces the stimulating effect that sodium chloride exerts when added alone to Pfeffer's solution. This is not a case of antagonism in the usual sense; but it is similar to the

action of calcium chloride in decreasing a stimulation of root growth produced by manganese chloride, which was termed antagonism by Barton and Trelease (1927). The results of Lipman (1909, 1910), Winslow and Falk (1923a, 1923b), and Gustafson (1920) on antagonism cannot be compared with the present work, as they were studying lessened toxicity—not diminished stimulation.

The next experiment to be considered is one which was planned in order to determine whether calcium would have any influence upon the
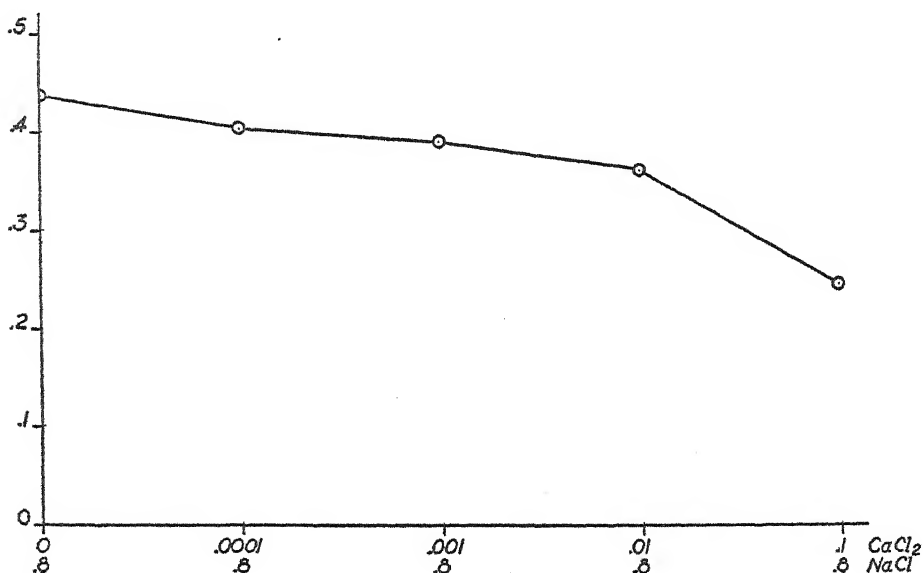
Fig. 9. Dry weights of felts of *Aspergillus niger* grown in Pfeffer's solution containing calcium chloride and sodium chloride. Each culture contained 0.8 M sodium chloride. Abscissas represent molar concentrations of calcium chloride (logarithmic scale). Ordinates represent weights of felts in grams. Control culture without sodium or calcium chlorides gave yield of 0.292 gram.

well known zinc stimulation of *Aspergillus*. Raulin (1869) was the first to observe that zinc sulphate, in very small amounts, has a striking effect in stimulating the mycelial growth of *Aspergillus*, and this phenomenon has since then been observed and studied by many other workers. It is noteworthy that, although the dry weight of the mycelium is greatly increased by minute quantities of zinc, the production of conidia is decreased, frequently to the point of complete inhibition.

In order to see if calcium chloride would have any influence upon this stimulation, *Aspergillus niger* was grown in Pfeffer's solution to which zinc sulphate and this salt were both added. A concentration of 0.00001 M

zinc sulphate was chosen for this experiment because it was found to give a very heavy, wrinkled, white felt, with sparse fruiting; the fungous felt was thick, opaque; and yet brittle. Calcium chloride, in concentrations ranging from zero to 0.2 M, was added to Pfeffer's solution containing this concentration of zinc sulphate. The results of this experiment are presented in the graph of figure 10, plotted from the data given in table 11.

TABLE 11

Influence of calcium chloride upon the growth of Aspergillus niger in Pfeffer's solution contaning a stimulating concentration of zinc sulphate.

CONCENTRATIONS		DRY WEIGHT OF MYCELIUM[a]
ZnSO₄	CaCl₂	
M	*M*	*Grams*
Zero	Zero	.283[b]
.00001	Zero	.684
.00001	.0125	.446
.00001	.025	.439
.00001	.05	.415
.00001	.1	.373
.00001	.2	.367

[a] Each value represents the mean for 9 cultures.

[b] Control culture.

Inspection of figure 10 shows that when calcium chloride was added to solutions having this concentration of zinc sulphate, the growth stimulation was greatly decreased. Even the addition of the lowest concentration of calcium chloride—namely, 0.0125 M—caused a pronounced drop in the dry weight of the fungus felt. The slope of the curve beyond this point is much more gradual, and even with the highest concentration of calcium chloride the dry weight was above that of the control culture (receiving neither zinc sulphate nor calcium chloride). The felts of the cultures that were supplied with calcium chloride and zinc sulphate were more abnormal in appearance than those to which zinc sulphate alone was added. They were soggy and sank in the liquid, and they exhibited no fruiting.

The combination, then, of zinc sulphate and calcium chloride was not favorable to *Aspergillus*. Calcium chloride alone in Pfeffer's solution had no appreciable effect on the growth or the fruiting of *Aspergillus*. Zinc sulphate alone in Pfeffer's solution greatly stimulated the production of dry material, and in the concentration used (0.00001 M) allowed some fruiting. The mixture of the two salts in Pfeffer's solution, however, had a distinctly harmful effect. The stimulation of mycelial growth was greatly lowered; the felts had an abnormal appearance, and they showed no signs

of sporulation. The study of Hawkins (1913), referred to in the introduction to this paper, involved an inhibition of the germination of the spores of certain fungi by salts of zinc and other metals. Antagonism was definitely shown by the fact that the addition of calcium allowed the spores to germinate. This study cannot be compared to the experiment just described, as zinc in the concentrations used does not inhibit the growth of *Aspergillus*, but on the contrary stimulates it.
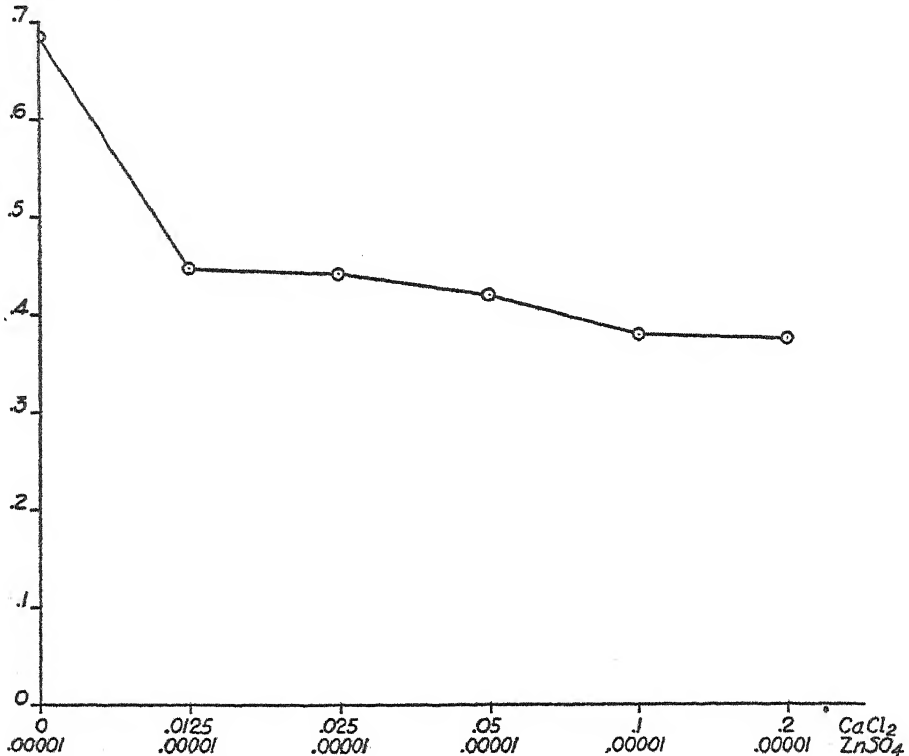
Fig. 10. Dry weights of felts of *Aspergillus niger* grown in Pfeffer's solution containing calcium chloride and zinc sulphate. Each culture contained 0.00001 M zinc sulphate. Abscissas represent molar concentrations of calcium chloride (logarithmic scale). Ordinates represent weights of felts in grams. Control culture without zinc sulphate or calcium chloride gave yield of 0.283 gram.

Influence on the growth of Aspergillus niger of varying the proportions of the three salts of Pfeffer's solution

In the experiments thus far described, the standard Pfeffer's solution was employed in all cases as a basic culture medium. The effects of varying the concentration of magnesium sulphate and of adding salts of calcium and other elements was studied; but no attempt was made to vary in a

systematic manner the proportions of all three component salts of Pfeffer's solution. To obtain further information concerning the salt requirements of *Aspergillus*, it seemed important to study the relations between the growth of the fungus and the proportions of the salts of Pfeffer's solution. The present section of this paper describes three experiments that dealt with this phase of the problem. The first two were concerned with the effects of varying the proportions of the three component salts, and the third involved the influence of calcium chloride upon the physiological values of the culture solutions.

Very few descriptions have appeared in the literature of experiments on fungi in which the proportions of the salts making up a nutrient solution have been varied. The researches along this line carried on by Tottingham (1914) and by Shive (1915) with green plants are so well known that they will not be discussed here. Dunn (1921) and Young and Bennett (1922) performed some similar experiments with fungi. Haenseler (1921) varied the salt proportions of the nutrient solution for *Aspergillus niger*, using calcium nitrate, monopotassium phosphate and magnesium sulphate for the three component nutrient salts; and in a repetition of the experiment he substituted sodium nitrate for calcium nitrate. Haenseler found that the partial concentrations of magnesium sulphate and potassium phosphate could be varied within wide limits without in any way affecting the yields. Steinberg (1919), in a much smaller series of tests, obtained different results. He observed an increased yield with increased amounts of either magnesium sulphate or potassium phosphate.

In the experiments to be described here, the proportions of the three salts of Pfeffer's solution were varied, but the total salt concentration was always kept at 0.1718 M, which is the gram-molecular concentration of the standard solution. The sugar was supplied in the usual concentration of 0.1461 M, or 50 grams per liter. The volume-molecular proportions of the salts for each culture and the corresponding dry weights of the felts are presented in table 12. The table also gives these weights as relative values calculated as a percentage of the highest weight obtained in the series. The equilateral triangle of figure 11 shows each of these percentages placed above and weights placed below the point representing the composition of the solution.

The proportions of the salts are represented on the triangle in the following manner: The upper apex of the triangle represents a solution in which 100 per cent of the dissolved molecules are potassium phosphate. The opposite base represents solutions containing no potassium phosphate. The right apex in the same manner denotes a solution in which 100 per cent of the dissolved molecules are ammonium nitrate, and that on the

left designates one in which 100 per cent are magnesium sulphate. The base opposite each apex represents a solution containing none of the salt represented at the apex. The exact center of the triangle represents a solution containing equal proportions of the three salts, and all other points inside the triangle represent solutions containing mixtures of the three salts. The proportions denoted by any point may be found by measuring the perpendicular distance of the point from each of the three bases.

TABLE 12

Influence on the growth of Aspergillus niger of varying the proportions of the three salts of Pfeffer's solution.

RELATIVE VOLUME-MOLECULAR PROPORTIONS OF SALTS[c]			DRY WEIGHT OF MYCELIUM[a]	
KH_2PO_4	NH_4NO_3	$MgSO_4$	Actual	Relative
			Grams	*Per cent*
5.0	5.0	90.0	.438	94
5.0	47.5	47.5	.321	69
5.0	90.0	5.0	.200	43
15.0	15.0	70.0	.465	100
15.0	70.0	15.0	.293	63
21.4	72.7	5.9	.296[b]	64[b]
33.3	33.3	33.3	.410	88
47.5	5.0	47.5	.374	80
47.5	47.5	5.0	.289	62
70.0	15.0	15.0	.348	75
90.0	5.0	5.0	.277	60

[a] Each value represents the mean for 6 cultures.

[b] Control culture, supplied with same concentrations as in Pfeffer's solution. Value represents the mean of 12 cultures.

[c] Total salt concentration, 0.1718 M.

It may be seen from figure 11 that the highest yields of *Aspergillus niger* (represented by 100 and 94 on the triangle) were obtained with high proportions of magnesium sulphate combined with low proportions of the other two salts. Thus, the growth of the fungus, as indicated by the amount of mycelium formed, was favorably influenced by a high proportion of magnesium sulphate in the nutrient solution. The solution giving the highest weight had the molecular proportions: KH_2PO_4, 15; NH_4NO_3, 15; $MgSO_4$, 70. These figures represent percentages of a total salt concentration of 0.1718 M. The corresponding molecular concentrations of the salts are as follows: KH_2PO_4, 0.02577 M; NH_4NO_3, 0.02577 M; $MgSO_4$, 0.12026 M. The heavy felts produced in this solution were somewhat wrinkled, apparently because there was not room in the flask for such large felts to lie flat; but they were very black and well fruited. The growth was therefore a healthy one.

The growth of the fungus was not favorably influenced by high proportions of ammonium nitrate or of potassium phosphate. The lowest weight of the series, 43 per cent of the best, was obtained in a solution containing the highest tested partial concentration of ammonium nitrate. The next to the lowest weight obtained in this series, 60 per cent of the best, is shown for felts grown in the solution having the highest concentration of potassium phosphate.
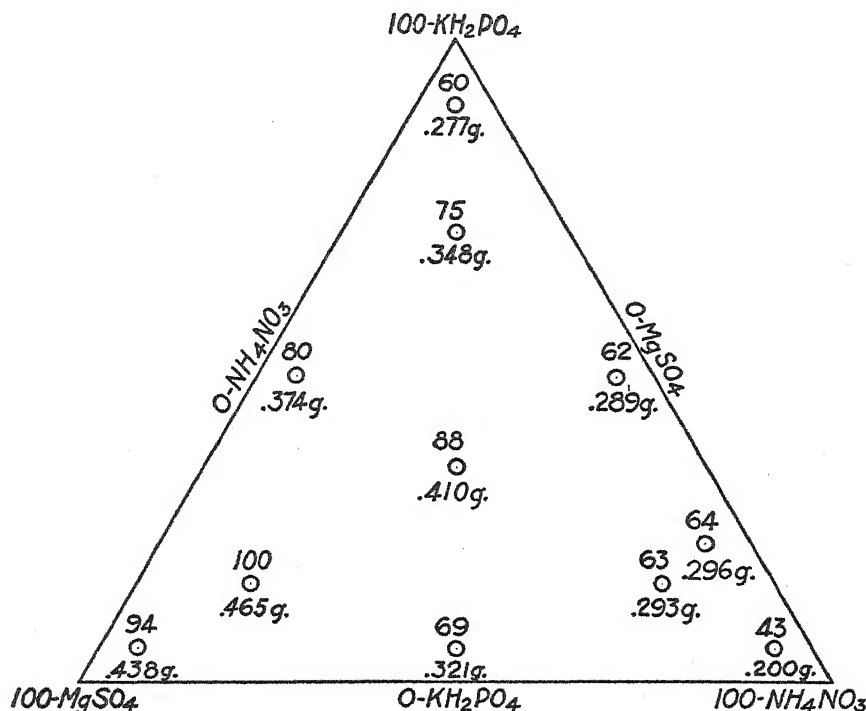
Fig. 11. Relative and actual dry weights of felts of *Aspergillus niger* as influenced by varying the proportions of the three salts of Pfeffer's solution. Upper numbers denote percentages of highest weight taken as 100; lower numbers denote actual weights, for culture solutions whose compositions are indicated by the positions of the points in the triangle.

It will be noticed that the control culture, containing the three salts in the same proportions as in Pfeffer's solution, gave only 64 per cent of the best growth. This solution has only a slightly higher proportion of potassium phosphate than the solution giving the best growth. It is characterized, however, by a much lower proportion of magnesium sulphate and a much higher proportion of ammonium nitrate. The low yield of this culture in comparison with that of the best culture indicates the marked

improvement that can be brought about by altering the salt proportions of Pfeffer's solution. It is clear that a solution containing more magnesium sulphate and less ammonium nitrate than are to be found in Pfeffer's solution gives much better growth of *Aspergillus niger* than is given with the

TABLE 13

Influence on the growth of Aspergillus niger of varying the proportions of the three salts of Pfeffer's solution.

RELATIVE VOLUME-MOLECULAR PROPORTIONS OF SALTS[c]			DRY WEIGHT OF MYCELIUM[a]	
KH_2PO_4	NH_4NO_3	$MgSO_4$	Actual	Relative
			Grams	*Per cent*
5.0	5.0	90.0	.615	92
5.0	25.0	70.0	.669	100
5.0	47.5	47.5	.561	84
5.0	70.0	25.0	.410	61
5.0	90.0	5.0	.245	37
15.0	15.0	70.0	.648	97
15.0	30.0	55.0	.615	92
15.0	55.0	30.0	.388	58
15.0	70.0	15.0	.298	44
20.0	40.0	40.0	.527	79
21.4	72.7	5.9	.347[b]	52[b]
25.0	5.0	70.0	.508	76
25.0	25.0	50.0	.466	70
25.0	50.0	25.0	.406	61
25.0	70.0	5.0	.297	43
30.0	15.0	55.0	.500	75
30.0	55.0	15.0	.360	54
33.3	33.3	33.3	.453	68
40.0	20.0	40.0	.540	81
40.0	40.0	20.0	.387	58
47.5	5.0	47.5	.449	67
47.5	47.5	5.0	.391	57
50.0	25.0	25.0	.396	59
55.0	15.0	30.0	.412	61
55.0	30.0	15.0	.459	69
70.0	5.0	25.0	.395	59
70.0	15.0	15.0	.444	66
70.0	25.0	5.0	.443	66
90.0	5.0	5.0	.300	45

[a] Each value represents the mean for 2 cultures.

[b] Control culture, supplied with same concentration as in Pfeffer's solution.

[c] Total salt concentration, 0.1718 M.

use of Pfeffer's solution. The amount of potassium phosphate, however, in this solution seems to be favorable.

The results of Dunn (1921) working with plus and minus strains of *Rhizopus* were markedly different from these. The solution in which she

obtained the best growth of both strains contained about equal molecular proportions of ammonium nitrate and magnesium sulphate, and a partial concentration of monopotassium phosphate about six times as great as that of either of the other two. Steinberg (1919) thought that the increased yield which he observed with large amounts of magnesium sulphate was due to iron impurities in this salt; but Currie (1917) found that iron did not increase the growth of *Aspergillus niger* when the nutrient solution was supplied with ammonium nitrate.
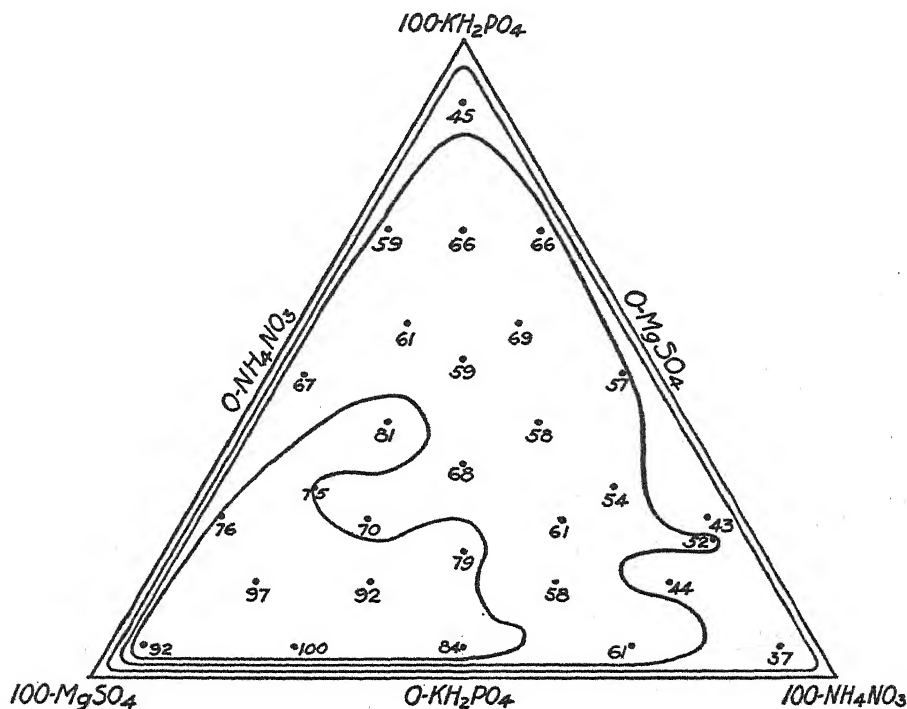
Fig. 12. Relative weights of felts of *Aspergillus niger* as influenced by varying the proportions of the three salts of Pfeffer's solution. Numbers denote percentages of highest weight taken as 100. Points in triangle indicate compositions of culture solutions. Contour lines divide area of triangle into the following zones: 0 to 25; 25 to 50; 50 to 75; 75 to 100.

The experiment just described was repeated on a more extensive scale by means of a duplicated series in which twenty-nine different sets of salt proportions were tested. These included eighteen new solutions in addition to the eleven that had previously been employed. The results of this experiment appear in table 13 and are represented graphically in the triangle of figure 12.

After expressing the dry weights of the felts as percentages of the heaviest, the resulting relative weights were divided into four groups: (1) from 75 to 100 per cent of the heaviest, (2) from 50 to 75, (3) from 25 to 50, and (4) from zero to 25. Contour lines were drawn on the triangle to include the ranges of values just indicated. The two outer zones of course are only rough approximations. In drawing the contour line that separates them it was assumed that each of the three sides of the triangle would represent zero growth; this seemed justified since it had been found by experiment that *Aspergillus* gave no growth if supplied with only two of the salts of Pfeffer's solution. The other two zones, however, seem to be fairly well defined by the numerous yield values which they include.

TABLE 14

Influence on the growth of Aspergillus niger of varying the proportions of the three salts of Pfeffer's solution with calcium chloride present in addition to the three salts.

RELATIVE VOLUME-MOLECULAR PROPORTIONS OF SALTS[c]			CONCENTRATION OF CaCl₂	DRY WEIGHT OF MYCELIUM[a]	
KH₂PO₄	NH₄NO₃	MgSO₄		Actual	Relative
			M	*Grams*	*Per cent*
5.0	5.0	90.0	.0625	.503	93
5.0	47.5	47.5	.0625	.359	67
5.0	90.0	5.0	.0625	.255	47
15.0	15.0	70.0	.0625	.539	100
15.0	70.0	15.0	.0625	.307	57
21.4	72.7	5.9	Zero	.291[b]	54[b]
33.3	33.3	33.3	.0625	.366	68
47.5	5.0	47.5	.0625	.256	48
47.5	47.5	5.0	.0625	.255	47
70.0	15.0	15.0	.0625	.323	60
90.0	5.0	5.0	.0625	.203	38

[a] Each value represents the mean for 6 cultures.

[b] Control culture, supplied with same concentrations as in Pfeffer's solution. Value represents the mean for 12 cultures.

[c] Total salt concentration without CaCl₂, 0.1718 M.

It will be noticed that the zone of high yields is in the lower left-hand corner of the triangle, corresponding to relatively high proportions of magnesium sulphate combined with low and medium proportions of the other two salts. The distribution of dry yields exhibits in general a satisfactory agreement with that obtained in the preceding experiment. The highest yield (indicated by 100 in the triangle) was obtained with a solution which had not been used in the preceding experiment; it contained less potassium phosphate than the best solution of the former experiment. But the solution that had been best in the preceding experiment gave a relative yield of 97 in the present experiment. The difference between the values 100

and 97 is so small that it is probably not significant. The control culture, supplied with the standard Pfeffer's solution, had a relative dry yield of only 52 per cent of that secured with the best solution. The results of this more extensive experiment show clearly, as do those represented graphically in figure 11, that the proportions of Pfeffer's solution can be improved for the growth of *Aspergillus* by increasing the partial concentration of magnesium sulphate and decreasing that of ammonium nitrate.
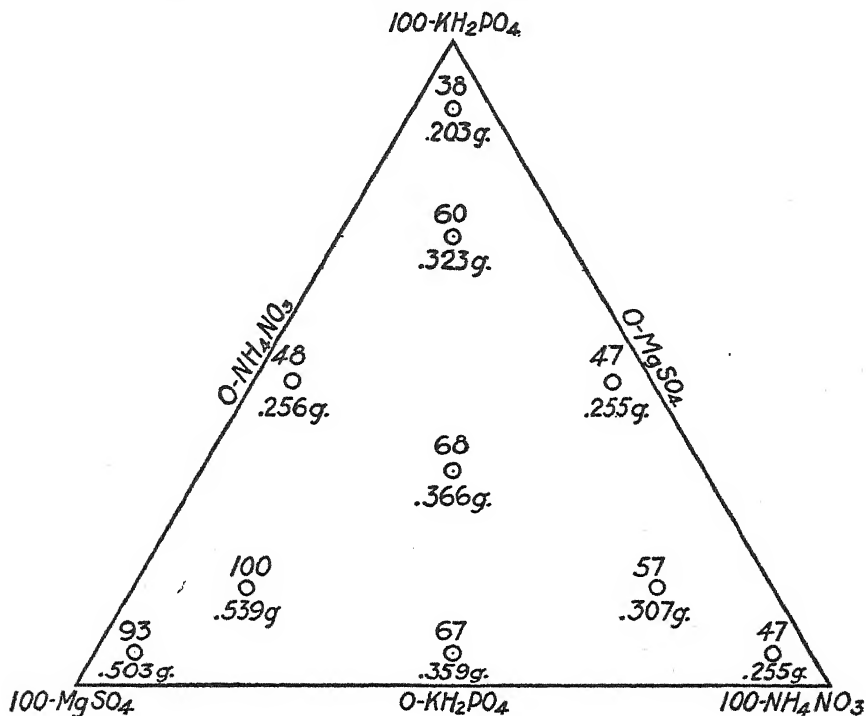
Fig. 13. Relative and actual dry weights of felts of *Aspergillus niger* as influenced by varying the proportions of the three salts of Pfeffer's solution, when each culture solution contained 0.0625 M calcium chloride. Upper numbers denote percentages of highest weight taken as 100; lower numbers denote actual weights, for culture solutions whose compositions are indicated by the positions of the points in the triangle.

A third series of cultures was conducted in an attempt to determine whether the addition of calcium chloride to the culture solutions would influence the distribution of dry yields, as these are related to the molecular proportions of the three salts of Pfeffer's solution. For this purpose calcium chloride in a concentration of 0.0625 M was added to each of ten culture solutions in which the proportions of the salts were varied in the same way as in the first experiment. The results of growing *Aspergillus* in these solutions are given in table 14 and are shown graphically in the

triangle of figure 13. A comparison of the three sets of triangular graphs—
the first two for solutions lacking calcium and the last for those containing
this element—fails to reveal any differences, either in the distribution of
yields or in their absolute values, that can with certainty be ascribed to
the influence of calcium. Very high dry yields were obtained in the lower
left-hand corner of the triangle, both in the presence and in the absence
of calcium. Very low yields are indicated for the lower right-hand corner
and for the upper apex, with and without calcium. Such differences as
exist between the dry yields of the corresponding cultures appear to have
been due to the variability of the biological material rather than to the
presence or absence of calcium. Variations between the two series lacking
calcium are as great as those between either of these series and the series
containing calcium. In general the comparison of these three experiments
leads to the conclusion that calcium had no very pronounced influence
on the responses of the fungus to the main nutrient salts. The presence of
calcium chloride in the culture solution seemed to cause the fruiting to ap-
pear brownish in color, rather than black; hence calcium may tend to
increase the formation of the yellow pigment often seen in the hyphae of
this fungus, especially when the spores germinate on bread. Some of this
yellow pigment probably dissolves in the nutrient solution, giving it the
characteristic yellow appearance caused by the addition of a calcium salt.
Thom and Church (1926, p. 11) point out a relation between the produc-
tion of yellow colors and acid conditions of the substrata.

SUMMARY

Aspergillus niger and *Penicillium sp.* were grown in Pfeffer's solution
and in certain variations of this solution. The fungi were cultured in 150
cc. Pyrex flasks, *Aspergillus* in an incubator at 34°C. for 5 days, *Penicillium*
at a room temperature of about 22°C. for 6 days. The felts were placed
on weighed filter papers, dried at 65° to 70°C. for at least 3 days and
weighed. The weights of the felts and the appearance of the cultures, par-
ticularly with respect to conidium formation, were used as the basis for a
comparison of the physiological effects of the culture solutions. The prin-
cipal conclusions follow:

The weights of the felts alone could not be taken as a satisfactory cri-
terion of the development of these fungi without also taking into con-
sideration their fruiting.

Magnesium was found to be absolutely essential for the growth of both
Aspergillus and *Penicillium*. This element must be required for some im-
portant but as yet unknown physiological function; and for good growth
of the fungi it must be supplied in concentrations higher than 0.0001 gram
molecule per liter of the culture solution. Though obviously not required

for the production of chlorophyll in these fungi, magnesium is as indispensable for them as for the higher green plants. High concentrations of magnesium poison *Aspergillus* as they do the higher plants, but the minimum toxic concentration is greater for the fungus.

Spectrographic analysis showed that some calcium was present in the mycelium of *Aspergillus* grown in Pfeffer's solution that had been prepared with doubly distilled water and the best grade of salts obtainable. The fungus was evidently able to absorb small amounts of calcium which were supplied as an impurity in the mineral salts or sugar, or it derived these salts from the spores. Precipitation tests with sodium oxalate showed that the culture solutions contained less than 0.000001 M of a salt of calcium—that is, less than 1 part of calcium per 25 million parts of the culture medium. *Aspergillus* also was found to make excellent growth in a culture solution containing a very high concentration (0.1 M) of sodium oxalate, which presumably would precipitate all but exceedingly minute traces of calcium. These considerations lead to the conclusion that if calcium is essential for the development of *Aspergillus* it is needed only in extremely small quantities; the amount of calcium required—if any—is no greater than the quantity of boron, zinc, manganese, iron, or copper that is essential for the higher green plants and possibly also for the fungi.

Calcium chloride did not antagonize the poisoning of *Aspergillus* due to high concentrations of magnesium chloride in the culture solution. In a concentration of 0.1 M, it increased the toxic effect.

A stimulation of mycelial growth that resulted from addition of sodium chloride to the culture medium was decreased when calcium chloride was also added; but the addition of both of these salts produced felts which were more abnormal in appearance than those obtained by the addition of either salt alone to Pfeffer's solution.

Calcium chloride decreased the well-known stimulation of mycelial growth due to zinc sulphate; but the addition of these two salts had a decidedly toxic effect on the fungus felts, spore formation being suppressed much more than with either salt alone in Pfeffer's solution.

A marked improvement over the standard salt proportions of Pfeffer's solution was obtained by varying the three salts in a systematic manner. The growth of *Aspergillus niger* was greatest in solutions that contained higher proportions of magnesium sulphate and lower proportions of ammonium nitrate than those of Pfeffer's solution. The addition of a calcium salt seemed to have no pronounced influence on the growth responses of *Aspergillus* to the three main salts.

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The anatomy of the leaf of Panicum palmifolium

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(WITH THREE TEXT FIGURES)

In general every foliage leaf of the grass plant consists of two parts, the blade and the sheath. The ligule, which varies in size and shape, also occurs in most grass leaves. A petiole-like stalk is inserted between the blade and the sheath in the leaves of a few tropical and semi-tropical grasses, such as *Pharus*, *Phyllorachis*, *Olyra*, *Ischaemum*, many of the *Bambusae* and some of the species of *Panicum* (Hackel, 1890). The leaves of many of these plants have broad plicate blades.

The above mentioned features of the grass leaf are all exemplified in the leaf of *Panicum palmifolium* Willd.,[1] plants of which have been successfully grown in the greenhouse at Indiana University for many years. Because of the ease with which the plant can be grown, I have been able to get for this study all stages in the development from the seed to the adult plant.

The peculiar features of the leaf give rise to many questions, of which the following are examples: (1) Is the stalk of the leaf a real petiole? (2) What is the mode of development and the internal effect of the corrugations of the leaf? (3) What are the functions of the corrugations? (4) Is the venation of the leaf really pinnate? (5) How is the corrugated leaf related phylogenetically to the ordinary flat leaf of grasses?

LITERATURE

In the extensive literature on the anatomy of the grass leaf, some of these questions have already been considered as applied to other grasses. Duval-Jouve (1875) gives a summary of the work done up to 1865 making special mention of Scheuzcher, Babel and P. de Beauvois. Scheuzcher was the first botanist to divide the grass leaf into blade, sheath and ligule. P. de Beauvois (1822) supported a theory that Linnaeus set forth in the thesis of his student, H. Gahn. Linnaeus thought that all the leaves of grasses were similar in structure. This idea, resulting from insufficient study on the part of de Beauvois, hindered the investigations along this line for a long time. In 1865, Wiess saw the openings of the stomata and a few years later Pfitzer tried to explain the function and the make-up of the stomata.

Duval-Jouve was primarily interested in finding anatomical characteristics which would have taxonomic value. Pée-Laby (1898) carried this idea a step farther, attempting as he says in the introduction, to group the

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[1] *Chaetochloa palmifolia* (Willd.) Hitchc. & Chase.

grasses of France according to taxonomic characters of the leaves and to make known the physiological rôle of certain foliar tissues based upon the arrangement, the structure, and the development of their elements. The work done since 1865 on the grass leaf is summarized by Löv (1926) in a paper on the mechanism of the unfolding of the leaves of monocotyledonous plants.

<div align="center">GENERAL FORM OF THE LEAF</div>

At the present time, there are various theories as to the anatomical significance of the parts of the grass leaf. De Candolle's phyllode theory, also supported by Arber (1918), maintains that the monocotyledonous leaf does not correspond to the complete dicotyledonous leaf with its base, stipules, blade, and petiole, but is merely equivalent to the petiole and the sheathing base. Another theory championed by Bugnon (1921) holds that the blade is equivalent to the basal sheath of the leaf of the dicotyledon and that the sheath of the grass leaf is a new structure. A third and more common theory is that the parts of the grass leaf are the same as those of the dicotyledonous leaf; the sheath of the grass leaf is equivalent to the leaf base, and the ligule to the stipules; the blade is the same in both and the stalk present in some grass leaves is a true petiole (Hitchcock, 1922). It is not my purpose to give further evidence on the theories, but I shall use the nomenclature of the last mentioned.

The leaves of *Panicum palmifolium* have four distinct parts, sheath, petiole, ligule and blade. The broad blade tapers towards both ends to a general oblanceolate form. The upper surface is covered with fine velvety hair and the margin is minutely serrate. Its most striking feature is the series of oblique longitudinal folds which are especially prominent when the plant has insufficient moisture. There is a prominent midrib, and it continues in some of the leaves as a distinct petiole. In the case of the young plants, the petiole may be from two to four inches long but in the leaves formed later it is very short or entirely lacking. The ligule is made up of long hairs. The sheath is much like that of the other grasses.

The oldest tissues of a grass leaf are at the top and growth continues at the base long after the tip is mature. The fact that the leaf has a petiole, blade, sheath, and ligule that are so different from one another, raises the question as to how all of them could have grown from a single primordium in the bud. No attempt to answer this question will be made here.

<div align="center">THE CORRUGATIONS OF THE BLADE</div>

The development and the functions of the corrugations of the leaves of this kind have received attention from many workers. When the leaf emerges from the bud, it is folded flat as a fan and expands by a hinge ac-
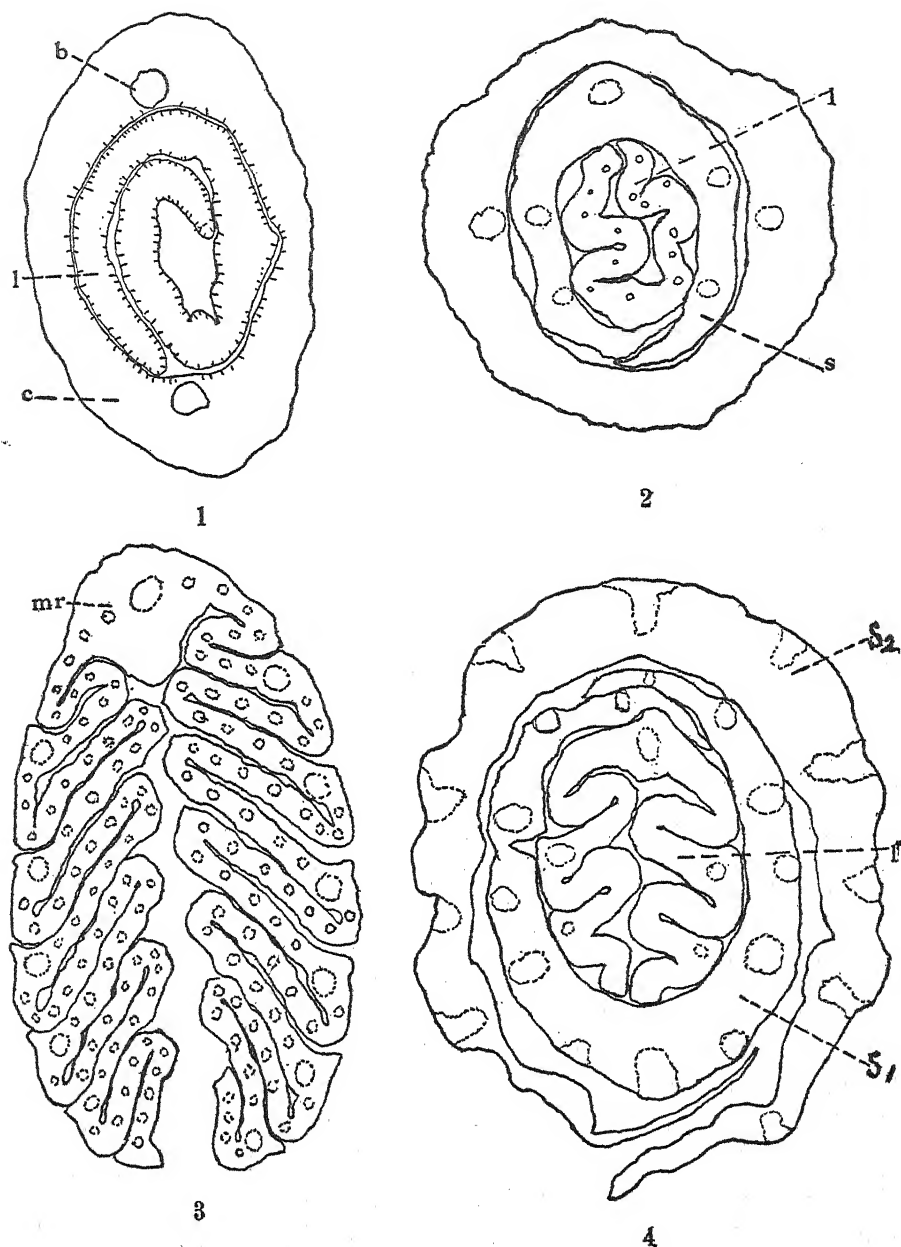
Figs. 1–4. 1. Cross section of a seedling showing juvenile leaf. *b*, fibrovascular bundle; *c*, coleoptile; *l*, juvenile leaf. Fig. 2. Cross section of a seedling showing the first folded leaf. *l*, first folded leaf; *s*, sheath of the juvenile leaf. Fig. 3. Cross section of a much later leaf still in the bud. The sheaths on the outside removed; *mr*, midrib. Fig. 4. Cross section of seedling showing third folded leaf. *s₂* sheath of first

tion of the folds. At the bottom of each groove is a line of bulliform cells which are ordinarily thought to bring about the folding and the unfolding of the blade by a response to the change of moisture.

Duval-Jouve would have one think that it is the retardation of the growth of the bulliform cells which gives rise to the folded vernation of the leaf in the bud. He finds evidence of this in the comparison of an adult leaf and a young leaf. Pée-Laby (1898) believes that Duval-Jouve has gone a little too far in giving the bulliform cells so much influence on the vernation of the leaf in the bud especially when they are not present or are scarcely visible. "Cependant, il est allé un peu loin, à mon avis, en leur attribuant une influence prépondérante dans la mode de vernation de la feuille en bouton, lorsque ces cellules n'existent pas encore ou sont à peine sensible." Both Duval-Jouve and Pée-Laby tell of the folding and the unfolding of the leaves when they mature, but they say nothing as to the initial unfolding. Löv believes that the initial expansion of the leaf is not the result of equal growth of all the cells but rather a rapid enlargement of more or less specialized cells which up to the time of unfolding have lagged behind the others in development.

To obtain some definite views on this problem, a study was made of the development of the leaves at five different stages: (1) a very young leaf in the bud, (2) an older stage in the bud, (3) a leaf that is coming out of the bud, (4) a leaf that is unfolding, and (5) a leaf that is unfolded.

The material was fixed, sectioned, and stained in the ordinary way and the results obtained were probably not dependent on any special feature of the method of procedure.

An examination of a very young leaf shows the cells all alike, with no differentiation among the tissues (fig. 2).[1] At the apex the blade is folded in the middle. As we approach the greatest width of the blade, the folds on each side of the midrib increase in number and then decrease again as we approach the base of the blade. The number of folds at this stage of development depends on the size of the leaf, that is, the small first leaves of the plants have fewer folds than the larger ones which follow them (figs. 3, 4).

The older leaves, still in the buds, show a beginning of the differentiation of the vascular tissue (fig. 4). The epidermal cells are all alike in contents; the only difference that is noticeable is that those in the folds are smaller.

When a portion of the leaf emerges from the bud, it shows a complete differentiation of all the main tissues (fig. 3). The epidermal cells are well

[1] All the figures pertain to *Panicum palmifolium* Willd. They are camera lucida drawings from microtome sections.

developed except for those that are found in the folds. These are still small
and full of dense protoplasm (fig. 6). It will be noticed that there are two
folds between each two adjacent large primary bundles (fig. 5). I am of the
opinion that this is the reason that both Duval-Jouve and Pée-Laby
thought they saw the bulliform cells. What they really saw was the group
of small cells at the base of the folds, which are later to become bulliform
cells.

The first step in the unfolding of the leaf is the spreading apart of the
two halves (fig. 7); this is a mechanical process that will occur whenever
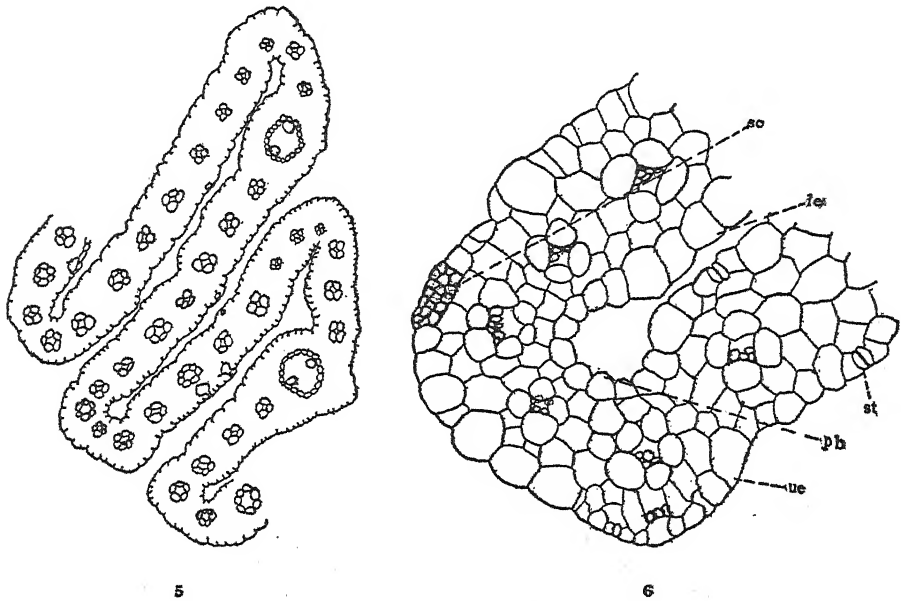
Figs. 5, 6. 5. A portion of fig. 3 enlarged. Fig. 6. A portion of fig. 5 enlarged;
le, lower epidermis; *pb*, primodial bulliform cells; *sc*, sclerenchyma tissue; *st*, stoma;
ue, upper epidermis.

the leaf obtains enough room. The other folds are still present. In the
parts of the leaves that have unfolded, it will be noticed that the small
cells which were in the folds have grown fourfold to tenfold making them
much larger than the rest of the epidermal cells; these are the bulliform
cells. The leaf is not regular in its method of unfolding. In some of the
leaves it begins in the center and in others at the ends; and sometimes it
is somewhere between. Though there is no regularity in the unfolding, the
bulliform cells of the upper epidermis develop before the corresponding
cells of the lower epidermis. The irregularity in the process of the unfolding

should be studied more carefully and more extensively before any conclusions are to be drawn from it.

A section of the adult leaf shows the typical ridges and grooves (figs. 8–11). How well defined the ridges and grooves will be depends on the condition of the plant when the leaves were fixed. A leaf that has fully turgid bulliform cells will be almost flat (fig. 11).

It is certain that the initial folds and the initial unfolding are not caused by the hygroscopic sensitiveness of the bulliform cells. The initial folds must be attributed to the crowded conditions in the bud and the initial unfolding to the rapid development of the bulliform cells which have been retarded in the limited space at the bottom of the grooves between the folds.

VENATION

The venation of the leaf is of interest because it appears to be pinnate. The corrugations extend obliquely from the midrib to the margin and the veins run into the midrib.

An examination of the sections shows that after the vein runs into the midrib it continues down the midrib without uniting with the other bundles. In a section of the midrib, the bundles are arranged in a crescent on the lower side. By counting, it is found that the number of main bundles at the base of the leaf, where the leaf is mostly petiole, is almost the same as the number found at the greatest width of the blade.

Several methods were tried in the attempt to prepare the whole leaf blade for a study of venation. The method that Evans (1928) used in his study of the bundles of the stem of *Zea Mays* did not prove successful because the amount of sclerenchyma makes the process of retting almost impossible. The best method found was to decolorize, stain and clear the leaf and then to examine at low magnification. The leaves were decolorized with alcohol and placed in anilin safranin for twelve or more hours. After sufficient destaining and dehydration with alcohol, they were gradually changed to xylol.

On the examination of these leaves, it was found that the veins were almost parallel to each other, and that most of them went into the midrib, and from there they went down the midrib as separate individuals. At the base of the blade a few veins were found to unite with others instead of going separately into the midrib. This is an indication of a tendency towards true pinnate venation. Besides these there are found in the leaf blade a great number of veinlets that merely provide cross connections between the main veins. In spite of these lateral unions of veins it seems that we have only a slight modification of the parallel venation common in other grasses.

PHYLOGENY

The folded leaf blade is an adaptation of the plant to a definite set of conditions. When the leaf is still in the bud, it is necessary that it be folded
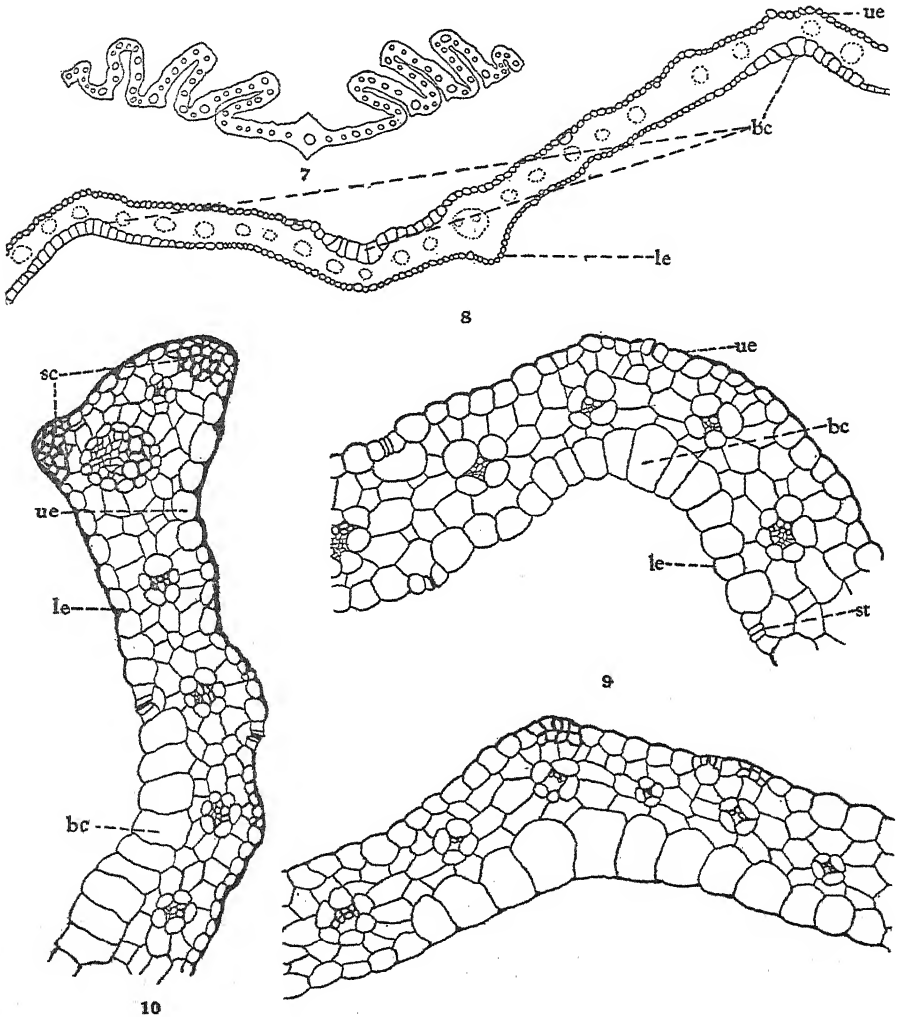
Figs. 7–11. 7. A cross section of a leaf that has emerged. Fig. 8. A portion of a cross section of a blade showing three groups of bulliform cells; *bc*, bulliform cells; *le*, lower epidermis; *ue*, upper epidermis. Fig. 9. Cross section of blade showing a group of bulliform cells. *bc*, bulliform cells; *le*, lower epidermis; *st*, stoma; *ue*, upper epidermis. Fig. 10. Cross section of the edge of the blade. *bc*, bulliform cells; *le*, lower epidermis; *sc*, sclerenchyma tissue; *ue*, upper epidermis. Fig. 11. Cross section of the blade showing a group of turgid bulliform cells.

to be accomodated to the small space. When it is fully developed the folds hold the blade rigid and prevent too rapid transpiration.

The folded leaf seems to be a characteristic of recent evolution as is seen in the seedling. The plant starts its growth like all other species of grasses. The first leaf of the seedling is rolled in the bud but flat after it emerges (fig. 1). The successive leaves gradually change from the flat type to one that is folded, each leaf being wider and having more folds than the one that precedes it. The increase in the number of folds is due to the fact that the broader leaf is in a bud that has increased very little in diameter.

The bulliform cells, as was said before, develop during the initial unfolding of the leaves; the juvenile leaf never forms any bulliform cells. In most grasses, these cells are developed only on the upper surface; but a few species, like the one under consideration, have bulliform cells on both sides of the blade. In any one part of the blade of *Panicum palmifolium* the bulliform cells of the upper surface develop before those of the lower surface.

These characteristics of the juvenile leaf and the order of the development of the bulliform cells do not *prove* anything but their close resemblance to the typical leaf structure of common grasses is cited as good evidence of the recent evolution of the plicate blade.

SUMMARY

1. The leaf of *Panicum palmifolium* has a broad plicate blade, short petiole, hairy ligule, and an ordinary sheath.

2. The leaf is folded conduplicately in the bud. This mode of vernation is caused by the crowded conditions that exist.

3. The initial unfolding of the leaf is caused by the *development* of the bulliform cells. The folding and the unfolding of an adult leaf is caused by the *hygroscopic sensitivity* of the bulliform cells.

4. The venation which superficially seems to be pinnate is not really pinnate. When the veins enter the midrib, they continue down the midrib as separate individuals. The superficial effect is caused by the oblique folds of the blades.

5. The features of the juvenile leaf and the order of the development of the bulliform cells seem to indicate that the plicate leaf is of recent origin.

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Studies of South American plants. II. New Loranthaceae and Monimiaceae from the northern Andes

Albert C. Smith

In the accompanying paper specimens from several herbaria are cited. The location of specimens is indicated by the following abbreviations: Botanisches Museum, Berlin-Dahlem (B); Conservatoire Botanique, Geneva (C); Royal Botanic Gardens, Kew (K); U. S. National Museum (N); New York Botanical Garden (Y).

Loranthaceae

Aetanthus colombianus sp. nov. Frutex parasiticus; ramis ramulisque subtriangularibus glabris crassis subrugosis; petiolis crassis rugosis anguste alatis ad 2 cm. longis; laminis crasse coriaceis ovato- vel obovato-ellipticis, 6–12 cm. longis, 2.5–7 cm. latis, basi attenuatis, apice rotundatis, margine integris, utrinque glabris et dense stomatiferis, pinnatinerviis, nervis secundariis 3–5-jugis adscendentibus utrinque leviter elevatis vel haud conspicuis; floribus in pseudocymis axillaribus dispositis; pedunculis primariis et secundariis 5–7 mm. longis, bracteis minute deltoideis; pedicellis binis 3–4 mm. longis; cupula subpatelliformi margine cartilaginea apice 3–4 mm. diametro; calyculo cylindrico apice patulo minute lobato, circiter 5 mm. longo, sub anthesi 1.5–2 mm. diametro; perigonio cylindrico carnoso coccineo, saepe distaliter luteo, maturitate 8–9.5 cm. longo, basi 1.5–2 mm. diametro, ad medium 6-lobato, lobis linearibus recurvatis, basi circiter 1.7 mm. latis, apice acutis; filamentis carnosis glabris prope basin loborum adfixis, 12–18 mm. longis; antheris erectis linearibus basifixis, 13–16 mm. longis, apice acutissimis et membranaceis, loculis eseptatis, ventralibus quam dorsalibus paullo longioribus, basi minute sagittato-divaricatis; stylo filiformi, stigmate ellipsoideo minute papilloso.

Type, *Killip & Smith 20583*, collected Mar. 12, 1927, along edge of woods on the eastern slope of Páramo del Hatico, between Pamplona and Toledo, Department of Norte de Santander, Colombia, alt. 2900 meters, and deposited in the herbarium of the New York Botanical Garden. Duplicate at N. Other collections, all from Colombia at altitudes of 2900–3600 meters, are: Norte de Santander: Páramo de Almuerzadero, *Linden 1348* (C). Ocaña, *Kalbreyer 438* (K). Santander: Western slope of Páramo Rico, *Killip & Smith 17795* (N, Y). La Baja, *Funck & Schlim 1406* (C); *Killip & Smith 18127* (N, Y). East of Las Vegas, *Killip & Smith 15810* (N, Y). It is a species of the section *Euaetanthus* Engl., related to *A. Mutisii* (H.B.K.) Engl., which has flowers 20 cm. long or more. The leaves of our species are proportionately narrower, but leaves throughout the genus are

very variable. The Peruvian *A. ornatus* Krause, the only other described species of this alliance, also has flowers longer than ours and leaves uniformly smaller.

Psittacanthus verticillatus sp. nov. Frutex parasiticus; ramulis subteretibus rugosis glabris, ad nodos incrassatis articulatis verticillatis, eis minoribus cum foliis saepe deciduis; petiolis incrassatis rugosis anguste alatis ad 8 mm. longis; laminis crasse coriaceis obovato-oblongis, 5–8 cm. longis, 3–5 cm. latis, basi attenuatis, apice rotundatis, margine integris, utrinque glabris et dense stomatiferis, obscure pinnatinerviis, nervis secundariis 2–4-jugis e costa prope basin saepe orientibus adscendentibus, cum costa haud conspicuis; inflorescentiis brevibus ad nodos dense aggregatis, ubique partibus exterioribus minute cinereo-pulverulentis, mox glabrescentibus; pedunculis subrugosis 3–7 mm. longis, bracteis parvis deltoideis; pedicellis binis 2–3 mm. longis; cupula patelliformi margine irregulari apice 3–4 mm. diametro; calyculo campanulato-cylindrico apice patulo margine irregulari, sub anthesi 6–7 mm. longo et 2.5–3 mm. diametro; perigonio cylindrico carnoso coccineo, maturitate 6–8.5 cm. longo, inferne circiter 2 mm. diametro, ad medium 6-lobato, lobis linearibus recurvatis, circiter 1.5 mm. latis, apice subacutis, margine ventrali crenatis; filamentis carnosis glabris circiter 25 mm. infra apicem perigonii adfixis, 9–12 mm. longis; antheris glabris prope basin dorsifixis, oblongo-linearibus, 10–12 mm. longis, apice obtusis; stylo perigonium aequante, stigmate ellipsoideo minute papilloso.

Type, *Killip & Hazen 9484*, collected Aug. 1 or 2, 1922, in forest below Magana, Quindio Trail, Department of Caldas, Colombia, alt. 3000–3200 meters, and deposited in the herbarium of the New York Botanical Garden. Duplicates at B, N. Another collection from Caldas is *Killip 9809* (N, Y), from Alaska, above Salento. Two other Colombian specimens without definite locality which may be placed here are: *Linden 704* (K), *1348* (K). It is a species of the Section *Arthraxon* Eichl., allied to the Ecuadorian *P. obovatus* (Benth.) Eichl., from which it differs by having the leaves somewhat larger and more noticeably attenuate at base and the flowers twice as long.

Phthirusa tortuosa sp. nov. Frutex parasiticus glaber; ramulis teretibus elongatis subscandentibus; petiolis gracilibus rugosis superne anguste alatis 5–9 mm. longis; laminis tenuiter coriaceis ovatis vel obovatis, 4–5.5 cm. longis, 2–3.5 cm. latis, basi attenuatis, apice plerumque acutis, margine integris et cartilagineis, utrinque stomatiferis, pinnatinerviis, costa utrinque elevata, nervis secundariis 2–4-jugis adscendentibus leviter elevatis; inflorescentiis ♂ racemosis axillaribus solitariis 3–6 cm. longis; floribus sessilibus in ternationibus pedunculatis dispositis, pedunculis rugosis 1–1.5 mm. longis; bracteis deltoideis acutis, maxima circiter 1.5 mm. longa et lata; calyculo cyathiformi truncato, circiter 1 mm. longo et 1.5 mm. diametro; perigonio ad basin 6–

lobato, lobis oblongis, circiter 3.5 mm. longis et 1 mm. latis, apice obtusis, sub anthesi reflexis; staminibus alternatim circiter 2.5 mm. et 3 mm. longis; filamentis pallidis carnosis eglandulosis 1.5–2 mm. longis; antheris ovoideis, connectivis carnosis apice subacutis 0.3 mm. productis; stylo perigonium subaequante, stigmate ovoideo papilloso.

Type, *Rusby & Pennell 377*, collected July 26, 1917, on the plain between Río Cabrera and Villaviejo, Department of Huila, Colombia, alt. 500–550 meters, and deposited in the herbarium of the New York Botanical Garden. It is of the alliance of *P. orinocensis* (Spreng.) Eichl., from which species it is distinguished by its more slender habit and shorter peduncles, which are surmounted by smaller bracts.

Phthirusa gonioclada sp. nov. Frutex scandens parasiticus glaber dioecus (?); ramulis 4-angulatis vel anguste 4-alatis elongatis; petiolis rigidis rugosis 6–14 mm. longis; laminis tenuiter coriaceis vel chartaceis ovatis, 3–6 cm. longis, 1.7–2.7 cm. latis, saepe complicatis, basi acutis vel obtusis, apice acutis saepe apiculatis, margine integris cartilagineis, utrinque stomatiferis, pinnatinerviis, costa supra plana subtus prominente, nervis secundariis 3–6-jugis patulis supra planis subtus elevatis, cum venulis anastomosantibus; inflorescentiis ♂ racemosis axillaribus solitariis 5–8 cm. longis; floribus sessilibus vel subsessilibus in ternationibus pedunculatis dispositis; pedunculis rugosis 3–6 mm. longis, bracteis deciduis lanceolatis ad 4 mm. longis subtentis; bracteis ad summum pedunculorum subcoriaceis deltoideis circiter 1.5 mm. longis; calyculo cyathiformi, 1.5–1.8 mm. longo, circiter 2 mm. diametro, margine membranaceis integris; perigonio carnoso albo, ad basin 6-lobato, lobis oblongis subacutis, circiter 4.5 mm. longis, 1.2–1.5 mm. latis; staminibus alternatim circiter 3.5 mm. et 4 mm. longis; filamentis carnosis stramineis eglandulosis; antheris ovoideis, connectivis apice acutis 0.3 mm. productis; stylo carnoso, stigmate ovoideo; inflorescentiis ♀ velut ♂ sed paullo brevioribus; floribus ♀ plus minusve velut ♂, pedunculis ut videtur basi ebracteatis; calyculo sub anthesi breviter cylindrico nigrescente, circiter 2.5 mm. longo et 2 mm. diametro, limbo brevissimo erecto integro; perigonii lobis reflexis; staminibus sterilibus tenuiter carnosis, apiculis deltoideis circiter 0.5 mm. longis coronatis; stylo carnoso perigonium subaequante, stigmate globoso papilloso.

Type, *Killip & Smith 20537*, collected Mar. 12, 1927, on open hillside on the western side of Culugá Valley, north of Labateca, Department of Norte de Santander, Colombia, alt. 1480—1550 meters, and deposited in the herbarium of the New York Botanical Garden. Duplicate at N. The type collection bears ♂ flowers. Another collection, also from Norte de Santander, which bears ♀ flowers, is: dense woods in Pica-Pica Valley, above Tapatá, north of Toledo, alt. 2100–2400 meters, *Killip & Smith 20020* (N, Y). It is a species characterized by angled branchlets, long

peduncles often subtended by bracts, and acute long-petioled leaves. Like
P. tortuosa, it is related to *P. orinocensis* (Spreng.) Eichl. From both of
these species, *P. gonioclada* is distinguished by the first two characters
above mentioned and also by the larger flowers. The bracts of the ♀ in-
florescence are apparently lacking, while those of the ♂ are quite promi-
nent.

Struthanthus calophyllus sp. nov. Frutex scandens parasiticus glaber
dioecus; ramulis elongatis subteretibus vel leviter angulatis lenticellosis;
petiolis rugosis 4–5 mm. longis superne anguste alatis; laminis papyraceis
ovatis vel ovato-oblongis, 6–10 cm. longis, 3–5 cm. latis, basi rotundatis
vel obtusis, apice breviter acuminatis (apice ipso rotundatis et apiculatis),
margine integris, utrinque stomatiferis, pinnatinerviis, costa supra elevata
subtus prominente, nervis secundariis 4- vel 5-jugis adscendentibus, saepe e
costa prope basin orientibus, utrinque elevatis, venulis utrinque conspicuis
copiose reticulatis; inflorescentiis ♂ desideratis; inflorescentiis ♀ 2–4 in axil-
lis foliorum, ternationibus pedunculatis in racemos vel pseudocymas dispositis,
pedunculis circiter 3 mm. longis; floribus sessilibus vel eis lateralibus breviter
pedicellatis, pedicellis ad 1 mm. longis, bracteis ovato-deltoideis circiter 0.7
mm. longis; calyculo breviter cylindrico, circiter 1.5 mm. longo et 1 mm.
diametro, limbo brevissimo erecto 6-apiculato; perigonio carnoso luteo-viridi,
circiter 4.5 mm. longo, 6-lobato, lobis oblongo-linearibus subacutis, 0.4–0.5
mm. latis; staminibus abortivis prope apices loborum adnatis, circiter 1 mm.
longis; stylo carnoso, quam perigonio paullo breviori, stigmate subcapitato
minute papilloso.

Type, *Killip & Smith 16689*, collected Jan. 5 or 6, 1927, along edge of
forest in Río Suratá Valley, above Suratá, Department of Santander,
Colombia, alt. 2000–2300 meters, and deposited in the herbarium of the
New York Botanical Garden. Duplicate at N. It is a species of the rela-
tionship of *S. dichotrianthus* Eichl., from which it differs by its larger
papyraceous leaves, of which the venation is very prominent.

Oryctanthus lucarquensis (H.B.K.) comb. nov. *Loranthus lucarquensis*
H. B. K. Nov. Gen. & Sp. **3**: 440. 1818. *Phthirusa lucarquensis* G. Don Gen.
Syst. **3**: 421. 1834.

This species, known from the Province of Loja, Ecuador, falls into the
Section *Cladocolea* (v. Tiegh.) Engl. of *Oryctanthus*. The section is also rep-
resented by five Central American species.[1]

Oryctanthus Archeri sp. nov. Frutex scandens parasiticus glaber; ramulis
elongatis teretibus lenticellosis; petiolis rugosis canaliculatis suboppositis
7–9 mm. longis; laminis coriaceis ovato-oblongis, 5.5–7 cm. longis, 3–4 cm.

[1] Engl. & Prantl Nat. Pfl. Nachtr. III.1: 135. 1897.

latis, basi rotundatis, apice breviter acuminatis, margine integris, utrinque minute stomatiferis, pinnatinerviis, costa supra leviter impressa subtus prominente, nervis lateralibus 3- vel 4-jugis saepe e costa prope basin orientibus adscendentibus utrinque leviter elevatis, venulis reticulatis elevatis vel inconspicuis; inflorescentiis spicatis 2–5 in axillis foliorum 1.5–3 cm. longis 10–15-floris; floribus solitariis sessilibus, bracteis deciduis ovatis ad 2.5 mm. longis subtentis; calyculo breviter cylindrico vel cyathiformi, sub anthesi circiter 1.5 mm. longo et lato, limbo brevi erecto membranaceo subintegro vel minute 4-apiculato; perigonio carnoso ad basin 4-lobato, lobis ovato-oblongis, circiter 2.8 mm. longis et 1.3 mm. latis, basi contractis, apice acutis; staminibus quam perigonio paullo brevioribus; filamentis lobis adnatis; antheris sessilibus deltoideo-ovoideis, 0.8 mm. longis, basi subcordatis, apice subacutis; stylo carnoso circiter 2 mm. longo, stigmate subtruncato; baccis ovoideis vel obovoideis ad 6 mm. longis, apice truncatis.

Type, *W. A. Archer 1521*, collected Jan., 1931, at La Sierra, 18 kilometers north of Medellín, Department of Antioquia, Colombia, alt. about 2000 meters, and deposited in the U.S. National Herbarium (no. 1,517,470). The collector notes that the flowers are dull yellow-green, the fruit rose-red when young, becoming blue with a grayish bloom. It is a species of the Section *Cladocolea* (v. Tiegh.) Engl., related to *O. lucarquensis* (H. B. K.) A. C. Smith, from which it differs by its larger leaves and longer spikes, which are aggregated rather than solitary. These two species, with solitary sessile tetramerous flowers subtended by single bracts, are readily distinguished from others of the family in South America.

MONIMIACEAE

Siparuna Archeri sp. nov. Frutex 2–4 m. altus; ramulis divaricatis subteretibus fuscescentibus minute stellulato-pilosis; petiolis subteretibus parce pilosis 4–7 mm. longis; laminis viridibus elliptico-oblongis, 15–20 cm. longis, 4.5–7 cm. latis, basi cuneatis vel acutis, apice acuminatis, margine subintegris, utrinque parce praecipue nervis pilos stellatos minimos gerentibus, pinnatinerviis, nervis lateralibus 12–15-jugis arcuato-adscendentibus prope marginem subanastomosantibus, cum costa supra elevatis subtus prominentibus, venulis copiose reticulatis utrinque elevatis; inflorescentia axillari cymosa brevi 3–7-flora; pedunculo 5–7 mm. longo, cum floribus plus minusve dense fusco-stellulato-piloso; pedicellis 1–3 mm. longis; floribus ♂ circiter 1.5 mm. diametro; tepalis erectis oblongis rotundatis incurvatis 0.8–1 mm. longis et latis, extra pilosis intus glabris; velo tenuiter carnoso angusto plano circiter 0.3 mm. lato; staminibus 10–12, exterioribus majoribus et exsertis, pallidis glabris tenuiter carnosis oblongis subacutis, maximis 0.8 mm. longis et 0.3 mm. latis; antheris filamenta aequantibus, poris ovalibus contiguis circiter 0.25 mm. longis; floribus ♀ sub anthesi quam ♂ paullo majoribus; tepalis eis ♂ similibus; velo conico-elevato 0.5 mm. longo, ore 0.2 mm. diametro; stylis 6–8

liberis recurvatis circiter 0.6 mm. exsertis; drupis coriaceis rugosissimis sub-
globosis circiter 1 cm. diametro.

Type, *W. A. Archer 1840*, collected in April or May, 1931, near Quibdó,
on Río Atrato, Intendencia of Chocó, Colombia, alt. about 60 meters, and
deposited in the U. S. National Herbarium (no. 1,518,730). The collector
notes that the fruit is cream-colored tinged with red, has a strong lemon
odor, and when ripe dehisces violently and irregularly. It is a species not
closely related to any known from Colombia, but allied to the Central
American *S. nicaraguensis* Hemsl., than which it has proportionately
narrower leaves with shorter petioles. The present species has smaller
flowers than *S. nicaraguensis*, the tepals more erect and more deeply dis-
tinct from one another, and the stamens nearly twice as many. From *S.
macrotepala* Perk., a Peruvian ally, the new species differs by its more
numerous lateral nerves, longer petioles, smaller tepals, etc.

SIPARUNA VENEZUELENSIS Perk. This species, previously known from
Fendler 2358 (type coll., a sheet of which is at K), from Colonia Tovar,
State of Aragua, Venezuela, proves to be fairly common in the Eastern
Cordillera of Colombia. Here it grows in dense wet woods of the temperate
zone, at altitudes of 2000–3000 meters, becoming a slender shrub up to 6
or 7 meters in height. It is represented by the following *Killip & Smith*
collections: Santander: Río Suratá Valley, above Suratá, *21161* (N, Y);
Western slope of Mt. San Vicente, near Charta, *18972* (N, Y); Southern
slope of Mt. San Martín, near Charta, *19150* (N, Y), *19177* (N, Y); Las
Vegas, *16039* (N, Y). On these specimens the ♀ flowers are somewhat more
mature than those of the type collection, demonstrating the enlargement
of tepals after anthesis to a size of 3 mm. by 1.5 mm.

Siparuna sinuata sp. nov. Frutex vel arbor parva; ramulis teretibus fuscis
glabris; petiolis rugosis oppositis vel suboppositis 7–14 mm. longis, superne
anguste alatis, alis parce pilosis; laminis chartaceis oblongis vel obovato-
oblongis, 7–10 cm. longis, 3–4 cm. latis, basi truncatis vel obtusis, apice
breviter acuminatis, apice ipso obtusis, margine irregulariter sinuato-crenula-
tis, utrinque glabris, pinnatinerviis, nervis lateralibus 7- vel 8-jugis arcuato-
adscendentibus prope marginem subevanescentibus, cum costa utrinque planis
vel leviter elevatis, venulis paucis planis; inflorescentiis ♂ in foliorum axillis
plerumque binis, maturitate 2–3 cm. longis 10–20-floris, glabris vel parcissime
cinereo-pilosis; pedicellis 1–4 mm. longis; floribus ♂ nigrescentibus sub-
coriaceis maturitate 4–5 mm. diametro, parce minute luteo-glandulosis;
receptaculis obconico-subglobosis supra medium limbo angusto 0.5 mm. lato
obtuse 6-gono (e tepalis connatis saepe parce setosis constante) circumdatis;
velo conico-elevato circiter 1.8 mm. longo, ore maturitate circiter 1.5 mm.
diametro; staminibus circiter 6 nigrescentibus, margine membranaceis, dor-

saliter parce glandulosis, oblongis, circiter 3 mm. longis, ad 1.8 mm. latis, apice subacutis; filamentis quam loculis triplo longioribus; poris ovalibus contiguis circiter 0.5 mm. longis; inflorescentiis ♀ et drupis desideratis.

Type, *R. A. Toro 1346*, collected Sept. 10, 1928, at San Roque, near Medellín, Department of Antioquia, Colombia, and deposited in the herbarium of the New York Botanical Garden. It is a species related to *S. venezuelensis* Perk., from which it differs by having the leaves rounded rather than acute at base, the margins sinuate rather than denticulate, the inflorescence longer and the tepals more reduced.

SIPARUNA PENNELLII Perk. Colombia: Antioquia: Valparaiso, near Medellin, *Toro 1378* (Y). Previously known from the Departments of Caldas and El Valle. Our specimen, the precise vegetative equal of earlier collections, is apparently the first collection of ♂ inflorescence, which is here described:

♂ inflorescences usually 2 in leaf axils, subglabrous (deciduously stellulate-pilose), 10–20 mm. long, 6–12-flowered; pedicels 1–3 mm. long; mature flowers about 3.5 mm. in diameter; tepals 6 (rarely 5), minute, fused into a narrow ridge about 0.4 mm. broad; receptacle obconical-subglobose, densely pale yellow-glandular within; velum conical-elevated, membranous, about 1.3 mm. long, the aperture 1–1.3 mm. in diameter; stamens about 7, at maturity exserted, densely pale yellow-glandular on both surfaces (glands sessile, 0.1 mm. in diameter), oblong or ovate, obtuse at apex, 2.5–2.8 mm. long, 1.5–2.3 mm. broad; filaments 2 or 3 times as long as anthers, membranous; pores oval, 0.5 mm. long, the valves contiguous in dehiscence.

Siparuna tapatana sp. nov. Frutex 3–5 m. altus; ramis elongatis gracilibus divaricatis; ramulis teretibus fuscis minute cinereo-stellulato-pilosis; petiolis oppositis vel suboppositis teretibus 7–15 mm. longis velut ramulis novellis pilosis; laminis papyraceis oblongis vel elliptico-oblongis, 12–15 cm. longis, 5–7 cm. latis, basi obtusis vel anguste subcordatis, apice acuminatis, margine irregulariter serratis (dentibus minute callosis 5 vel 6 per centimetrum), utrinque subglabris vel parce stellulato-pilosis, stellis secus nervos principales densioribus, pinnatinerviis, nervis lateralibus circiter 10-jugis patulis prope marginem adscendentibus et irregulariter anastomosantibus, cum costa supra planis subtus prominentibus, venulis reticulatis saepe supra occultis; inflorescentiis ♂ cymosis, cymis in foliorum axillis 1–3 paucifloris 10–15 mm. longis, juventute ubique dense fusco-stellulato-pilosis; pedicellis 4–6 mm. longis; floribus ♂ maturitate subglabris 2–3 mm. diametro; receptaculis obconico-subglobosis superne limbo angusto 0.5 mm. lato obtuse 5- vel 6-gono (e tepalis connatis constante) circumdatis; velo molliter carnoso glabro conico-elevato circiter 1.3 mm. longo, ore minuto circiter 0.4 mm. diametro; staminibus circiter 6 carnosis glabris eglandulosis oblongo-ovatis, circiter 2.5 mm. longis, 0.8–1.5 mm. latis, apice contractis sed obtusis; filamentis quam an-

theris duplo longioribus; antheris per poros ovales contiguos circiter 0.7 mm. longos dehiscentibus; floribus ♀ sub anthesi quam ♂ majoribus; pedicellis ad 12 mm. longis; tepalis quam eis ♂ majoribus carnosis deltoideis, circiter 0.8 mm. longis, 1–2 mm. latis; velo conico-elevato maturitate 0.5 mm. longo, ore circiter 0.4 mm. diametro; stylis 5–7 praeter apicem subcohaerentibus, circiter 1 mm. exsertis; drupis juvenilibus subglobosis glabris 5 mm. diametro.

Type, *Killip & Smith 20330*, collected Mar. 5 or 6, 1927, in woods on the western side of Culugá Valley, above Tapatá, north of Toledo, Department of Norte de Santander, Colombia, alt. about 2300 meters, and deposited in the herbarium of the New York Botanical Garden. Duplicate at N. Another collection, also from Norte de Santander, is: Woods along stream near Loso, north of Toledo, 2200–2400 m., *Killip & Smith 20399* (N, Y). The type collection bears ♂ flowers, the other here cited bears ♀. It is a species related to *S. Pennellii* Perk., from which it differs by having the leaves thinner in texture and more closely and conspicuously serrate and the young parts more noticeably pilose. In structure of the ♂ flowers the two species are closely allied; however, in *S. tapatana* the stamens are carnose and eglandular, while in *S. Pennellii* they are membranous and densely glandular. The ♀ flowers of the new species are more persistently pubescent than those of *S. Pennellii*.

Siparuna asterotricha sp. nov. Frutex; ramulis crassis rectis teretibus, pilis stramineis stellatis subtomentosis dense indutis (pilorum ramulis ad 0.5 mm. longis); petiolis suboppositis teretibus velut ramulis densissime tomentosis 7–12 mm. longis; laminis oblongis vel elliptico-oblongis, 11–13 cm. longis, 4–5.5 cm. latis, basi rotundatis vel obtusis, apice breviter caudato-acuminatis, margine sinuato-serratis (dentibus callosis 4–6 per centimetrum), utrinque praecipue nervis pilos stellatos 10–15-ramosos gerentibus, pilis supra circiter 0.4 mm. diametro et 4–7 per millimetrum quadratum, pilis subtus circiter 0.7 mm. diametro et 2–4 per millimetrum quadratum, pinnatinerviis, costa supra elevata subtus prominente, nervis lateralibus plerumque 10-jugis arcuato-adscendentibus, prope marginem subanastomosantibus, supra planis subtus elevatis, venulis obscure reticulatis; inflorescentiis axillaribus subspicatis solitariis vel binis 10–20-floris, partibus exterioribus pilis minutis dense stellato-tomentosis; pedunculo 2–3.5 cm. longo; pedicellis 3–6 mm. longis; floribus ♂ sub anthesi 4–7 mm. diametro; receptaculo obconico circiter 2 mm. longo et 3 mm. diametro; tepalis nigrescentibus patulis oblongis, circiter 2 mm. longis et latis, apice rotundatis, intus glabris; velo breviter cylindrico, circiter 1 mm. longo, margine integro et membranaceo; staminibus subcoriaceis 10–12 oblongis, exterioribus et maximis circiter 2.5 mm. longis et 1.5 mm. latis, per poros contiguos circiter 0.6 mm. diametro dehiscentibus; floribus ♀ desideratis; drupis coriaceis longipedicellatis subglobosis circiter 15 mm. diametro.

Type, *R. A. Toro 966*, collected Feb. 1, 1928, at Tamesis, near Medellín, Department of Antioquia, Colombia, and deposited in the herbarium of New York Botanical Garden. It is a very distinct species, characterized by the small leaf hairs, the size and distribution of which are remarkably uniform. From *S. Trianae* A. DC., probably its nearest ally, it is distinguished by the pubescence, the larger leaves, the longer inflorescence, and the larger tepals. The single fruit on the type specimen is found on an inflorescence which also bears ♂ flowers; ♀ flowers are lacking.

Siparuna elliptica sp. nov. Frutex; ramulis fuscis angulatis vel subteretibus, juventute pilis stellatis cinereis 1–2 mm. longis indutis, demum glabrescentibus; petiolis oppositis rugosis subteretibus velut ramulis juvenilibus pilosis 1.5–4 cm. longis; laminis papyraceis elliptico-oblongis 20–25 cm. longis, 13–16 cm. latis, basi rotundatis, apice rotundatis vel obtusis, margine sinuato-serratis (dentibus callosis 3–5 per centimetrum), supra praecipue nervis pilis simplicibus indutis demum glabrescentibus, subtus pilos stellatos ad 1 mm. latos gerentibus, pinnatinerviis, costa crassa utrinque prominente, nervis lateralibus 15–18-jugis rectis patulis prope marginem adscendentibus utrinque leviter elevatis, venulis copiose anastomosantibus utrinque leviter elevatis vel planis; inflorescentiis ♂ axillaribus solitariis vel binis cymosis ad 4 cm. longis 8–15-floris; pedunculo rugoso 1.5–2.5 cm. longo, pilis simplicibus vel stellatis piloso, pedunculorum ramulis apice 3- vel 4-floris; pedicellis 3–6 mm. longis; receptaculo obconico sub anthesi circiter 5 mm. longo et 4 mm. diametro, velut pedunculo molliter piloso; tepalis 5 carnosis nigrescentibus oblongis patulis, 4–5 mm. longis, 1.5–2 mm. latis, apice subacutis et minute calloso-mucronatis, maturitate utrinque glabris; velo membranaceo elevato-conico, circiter 2 mm. diametro, ore parvo; staminibus 7 vel 8 dorsaliter parce glandulosis oblongis vel ovatis, circiter 3 mm. longis, exterioribus ad 3 mm. latis, margine membranaceis, apice obtusis, per poros contiguos ad 1 mm. longos dehiscentibus; inflorescentiis ♀ et drupis desideratis.

Type, *R. A. Toro 401*, collected Aug. 20, 1927, at Titiribi, near Medellín, Department of Antioquia, Colombia, and deposited in the herbarium of the New York Botanical Garden. Doubtless larger leaves than those above described will be found on more mature specimens. It is a species related to *S. amplifolia* A. DC., from which it differs by having the pubescence less dense throughout, the tepals 5 rather than 3 or 4, and the receptacle soft pilose rather than densely hispid.

Siparuna huilensis sp. nov. Frutex dioecus; ramulis elongatis teretibus, pilis ferrugineis stellato-tomentosis deciduis ad 0.8 mm. longis ac etiam pilis brevioribus puberulis persistentibus indutis; petiolis plerumque ternatis subteretibus velut ramulis pubescentibus 10–20 mm. longis (raro 25 mm.); laminis chartaceis (senioribus coriaceis et bullatis) oblongis vel obovato-oblongis, 12–17 cm. longis, 5.5–7.5 cm. latis, apice subacutis vel breviter acumi-

natis, basi cuneatis (basi vera anguste truncatis vel subcordatis), margine subintegris vel crenato-serratis (dentibus 2–5 per centimetrum) saepe anguste revolutis, utrinque pilos stellatos 0.3–0.4 mm. diametro gerentibus, pinnatinerviis, nervis secundariis 9–11-jugis arcuato-adscendentibus, cum costa supra planis vel impressis subtus prominentibus, venulis reticulatis supra saepe impressis subtus leviter elevatis; inflorescentiis ♂ desideratis; inflorescentiis ♀ cymosis plerumque 2 vel 3 in axillis foliorum 5–10-floris; pedunculo gracili 1–3 cm. longo fusco-stellato-puberulo; pedicellis sub anthesi 3–5 mm. longis; floribus ♀ extus velut pedunculo puberulis demum glabrescentibus, receptaculo obconico sub anthesi circiter 2 mm. longo et 3 mm. diametro; tepalis 5 (raro 6) intus glabris patulis ovatis subacutis calloso-mucronatis, 1.5–2.5 mm. longis, 1.7–2 mm. latis; velo elevato-conico molliter carnoso glabro 1–1.5 mm. longo, ore circiter 0.4 mm. diametro; stylis circiter 8 nigrescentibus leviter cohaerentibus, circiter 1 mm. exsertis apice divaricatis; drupis coriaceis subglobosis ad 12 mm. diametro, pedicellis ad 20 mm. longis.

Type, *Rusby & Pennell 869*, collected Aug. 1–8, 1917, in forest east of Neiva, Department of Huila, Colombia, alt. 1800–2300 meters, and deposited in the herbarium of the New York Botanical Garden. Other collections from the same locality are: *Rusby & Pennell 583* (Y), *870* (Y). All three of these specimens are ♀ ; the latter bears somewhat smaller leaves than the type but is similar in other respects. The collectors note that the plant is aromatic and the tepals greenish-white. It is a species related to *S. Mutisii* (H.B.K.) A. DC., from which it differs by having its leaves larger, more persistently pilose, and with more numerous secondary nerves. The ♀ flowers of the new species have the velum conical rather than plane.

Siparuna pectinata sp. nov. Frutex dioecus 2–4 m. altus; ramulis paucis rectis divaricatis teretibus, pilis ferrugineis stellato-tomentosis circiter 0.5 mm. longis dense indutis; petiolis suboppositis subteretibus velut ramulis tomentosis 6–16 mm. longis; laminis oblongis, 8–15 cm. longis, 4.5–7 cm. latis, basi rotundatis vel subcuneatis, apice subacutis, margine prominenter crenatoserratis (dentibus irregularibus 3–7 per centimetrum, versus basin et summo petioli elongatis), utrinque praecipue nervis pilos stellatos 4–9-ramosos gerentibus, pilis supra circiter 0.8 mm. diametro et 2–4 per millimetrum quadratum, pilis subtus paullo majoribus, pinnatinerviis, costa supra leviter elevata subtus prominente, nervis lateralibus plerumque 9-jugis arcuato-adscendentibus supra planis subtus elevatis, venulis inconspicue reticulatis; inflorescentiis ♂ cymosis plerumque 2 vel 3 in axillis foliorum 8–15-floris (floribus mox deciduis), ubique partibus exterioribus pilis ferrugineis circiter 0.3 mm. longis dense et arcte stellato-tomentosis; pedunculo 4–10 mm. longo; pedicellis gracilibus 2–3 mm. longis; floribus ♂ sub anthesi circiter 3.5 mm. diametro, receptaculo 1–1.5 mm. longo; tepalis 5 vel 6 patulis deltoideis acutis basi connatis, 1–1.3 mm. longis, 1.5–2 mm. latis; velo plano intus glabro 1.3–1.5 mm. diametro, ore circiter 0.4 mm. diametro; staminibus 6–8, antheris sessilibus oblongis

circiter 1 mm. longis et latis, apice rotundatis vel obtusis, squamas castaneas minutas dorsaliter gerentibus, per poros circiter 0.3 mm. diametro dehiscenti-bus; inflorescentiis ♀ axillaribus brevibus plerumque solitariis 3–5-floris, velut ♂ tomentosis; floribus ♀ quam eis ♂ majoribus, sub anthesi 5–7 mm. diametro, receptaculo obconico circiter 2.5 mm. longo et diametro; tepalis 6 vel 7 patulis ovatis subacutis circiter 2 mm. longis et latis; velo molliter car-noso plano circiter 3 mm. diametro, ore minuto; stylis circiter 12 nigrescenti-bus erectis leviter cohaerentibus circiter 0.7 mm. exsertis.

Type, *Killip & Smith 21135*, collected Dec. 11–15, 1926, in woods on the northern slope of Mesa de los Santos, above Piedecuesta, Department of Santander, Colombia, alt. 1000–1500 meters, and deposited in the her-barium of the New York Botanical Garden. Duplicate at N. Another col-lection from the same locality is *Killip & Smith 15056* (N, Y). Description of ♂ flowers is from the type collection, of ♀ flowers from no. *15056*. Leaves of the ♀ plant appear to be slightly larger and more acute at base than those of the ♂ plant. It is a species readily distinguished by the exaggerated serrations at the base of the leaves, which are given a ragged appearance. The unusually close tomentum is also characteristic. It is not closely related to any Colombian species, but may be allied to the Central American *S. tetraceroides* Perk., from which, in addition to foliage char-acters, it differs by having the upper surface of tepals and velum densely tomentose rather than glabrous.

Siparuna subscandens sp. nov. Frutex subscandens 6–10 m. altus; ramulis elongatis teretibus, juventute pilis densis ferrugineis stellatis ad 0.3 mm. longis indutis, demum glabrescentibus; petiolis oppositis vel suboppositis canaliculatis dense et arcte ferrugineo-tomentosis 8–18 mm. longis; laminis elliptico-oblongis maturitate coriaceis, 8–16 cm. longis, 3.5–7 cm. latis, basi acutis vel subacutis, apice breviter acuminatis, margine crenatis (dentibus minute apiculatis 4 vel 5 per centimetrum), utrinque pilis stellatis circiter 0.3 mm. diametro ferrugineo-tomentosis, pinnatinerviis, nervis lateralibus 8–10-jugis rectis adscendentibus, cum costa supra subplanis subtus prominentibus, venulis reticulatis supra planis subtus elevatis; inflorescentiis ♂ axillaribus plerumque binis 6–12-floris; pedunculo 7–15 mm. longo velut ramulis fer-rugineo-tomentoso; pedicellis crassis 2–5 mm. longis; floribus ♂ extra dense tomentosis, receptaculo campanulato sub anthesi 1.5–2.5 mm. longo et 2.5–3 mm. diametro; tepalis 5 aequalibus erectis oblongis, 0.6–0.8 mm. longis, 1–1.5 mm. latis, apice rotundatis et apiculatis, intus glabris; velo plano molliter carnoso nigrescente glabro 1.8–2.5 mm. diametro, ore sub anthesi 0.5 mm. diametro; staminibus circiter 15 molliter carnosis fusco-castaneis luteo-glandulosis ovato-deltoideis, exterioribus et maximis 1.3–1.5 mm. longis et basi latis, apice acutis, per poros contiguos circiter 0.7 mm. longos de-hiscentibus; inflorescentiis ♀ et drupis desideratis.

Type, *W. A. Archer 1361*, collected at La Sierra, 18 kilometers north of Medellín, Department of Antioquia, Colombia, alt. about 2000 meters, and deposited in the herbarium of the New York Botanical Garden. Duplicate at N. It is a species related to *S. asperula* (Tul.) A. DC., which it closely resembles in foliage. However, the new species apparently never has the leaves ternate. From *S. asperula* it also differs by having the inflorescence longer, the velum of ♂ flowers glabrous, and the stamens twice as numerous.

Siparuna quadrangularis sp. nov. Frutex 1–2 m. altus; ramulis crassis quadrangulatis subnigrescentibus cinereo-stellato-pilosis (stellis ad 1 mm. latis); petiolis oppositis crassis angulatis vel subteretibus velut ramulis pilosis 2.5–5 cm. longis; laminis oblongis, 25–35 cm. longis, 16–20 cm. latis, basi rotundatis, apice (?, specimino nostro incompleto), margine irregulariter serratis (dentibus 3–5 per centimetrum), supra parce (nervis dense) stellato-pilosis, subtus pilis stellatis densis cinereis villosis indutis, pinnatinerviis, costa crassa supra elevata subtus prominentissima, nervis lateralibus 15–20-jugis patulis rectis supra planis vel elevatis subtus prominentibus, venulis copiose reticulatis supra planis subtus elevatis; inflorescentia ♂ desiderata; inflorescentia ♀ axillari brevi 2–5-flora; pedicellis 2–4 mm. longis; floribus ♀ ad summum tubi sub anthesi 2–2.5 mm. diametro, tubo cum pedicello dense stellato-piloso, stellis ad 0.5 mm. longis; tepalis 4 carnosis late ovatis, 3–4 mm. longis et latis, apice apiculatis, extra et margine parce pilosis intus glabris; velo carnoso glabro conico-elevato circiter 0.8 mm. longo, ore circiter 0.6 mm. diametro; stylis 10–12 liberis recurvatis circiter 1.3 mm. exsertis.

Type, *Hitchcock 21317*, collected Sept. 2, 1923, between Portovelo (Gold Mine near Zaruma) and El Tambo, Province of Oro, Ecuador, alt. 600–1000 meters, and deposited in the herbarium of the New York Botanical Garden. It is a species related to *S. eriocalyx* (Tul.) A. DC., and *S. gesnerioides* (H.B.K.) A. DC., from both of which it differs by having its branchlets quadrangular and its tepals apparently always 4 rather than 4 to 6. Compared with *S. eriocalyx*, the new species has the leaves larger and the tepals glabrous within; compared with *S. gesnerioides*, it has the inflorescence shorter and the styles about twice as many.

The New York Botanical Garden

Cultural races and the production of variants in Pestalozzia funerea[1]

CLYDE CHRISTENSEN[2]

(WITH SIX TEXT FIGURES)

INTRODUCTION

In 1929, in the course of a study of a leaf disease of longleaf pine (*Pinus palustris* Mill.), the writer frequently found *Pestalozzia funerea* Desm. growing saprophytically on those portions of the leaves which had been killed by *Septoria acicola* (Thüm). A large number of single spores of *P. funerea* were isolated, and it soon became evident that the species comprises many different cultural races. Not only were a considerable number of races isolated, but variants appeared frequently in some of the cultures. As the material seemed very interesting from a mycological viewpoint, a study was made of the different races and their tendency to produce variants.

MATERIAL AND METHODS

Cultures were made by cutting out small sections of the needles, surface sterilizing the sections, and placing them on malt agar in petri dishes. The fungus grew rapidly on the agar and within a week it produced an abundance of acervuli on the surface of the cultures. One hundred and fifty single spores were isolated, 125 from the acervuli on the needles of longleaf pine and 25 from acervuli produced in the cultures described above, most of them by the plate dilution method. The cultures derived from these were grown on agar slants in test tubes, and those which appeared to be different from each other were transferred in duplicate to malt agar in 200 cc. Erlenmeyer flasks, each containing 32 cc. of agar. When these flask cultures were compared with one another, striking differences were observed in rate of growth, appearance of mycelium, and production of spores.

In the 150 cultures, derived from single spores, fifteen different races were found, each of which could be distinguished from every other one by rate of growth, color and topography of the surface mycelium, the abundance, manner, and time of spore production, and color and morphology of spores.

To facilitate a comparative study, all of the parent cultures, obtained in the manner described above, and the sectors which appeared in these cultures, were transferred in duplicate to Coon's, Richard's, and malt agar in 200 cc. Erlenmeyer flasks.

<div align="center">GROWTH CHARACTERS</div>

In the cultures obtained from the pine needles at least a dozen very distinct races could be distinguished solely by their growth characters. To illustrate the differences between some of the races, several of them will be described as they appeared on malt agar, when the cultures were twelve days old.

Race 4: Mycelium in a dense flat mat; no aerial mycelium; three prominent concentric zones present, the outer one $\frac{1}{4}$ inch wide and white, the second one $\frac{1}{2}$ inch wide and pale yellowish brown, and in the center a lighter colored disc $\frac{1}{4}$ inch in diameter. No spores produced.

Race 6: Mycelium in a dense flat mat as in 4, but more scanty; uniformly yellowish brown, with a darker concentric band faintly visible in the center. Same rate of growth as 4. No spores produced.

Race 5: Mycelium white, abundant, appressed. Acervuli abundant in four broad concentric bands; acervuli very small, running together to form black, shiny, moist patches.

Race 18: Mycelium closely packed, grayish, aerial mycelium united into netlike tufts. Acervuli numerous, varying in size, evenly distributed.

Race 25: Mycelium with a pinkish tint, closely packed in a thick layer on the surface of the agar. Aerial mycelium united into tiny netlike tufts.

The above descriptions illustrate the method used in differentiating the races, but they hardly give an adequate conception of the degree of diversity of races on artificial media. Some of the races grew as much in three days as others did in three weeks; in some the mycelium was appressed, in others densely flocculent, in others woven into netlike tufts; in some the color was very white, in others a dirty grayish green, faint yellow, or delicate pink; in some races the growth was marked with rings, in others it was uniform throughout; some produced only a few spores, while in others the cultures were black with spores.

These races have been grown for more than a year on artificial media and few of them have shown any noticeable tendency to vary in a permanent way, except where sectors appeared. Their growth was different under different conditions, and on different media, but always, when returned to the medium upon which they were first grown, they displayed the characteristics of the original cultures. Six of the races are shown in figure 1.
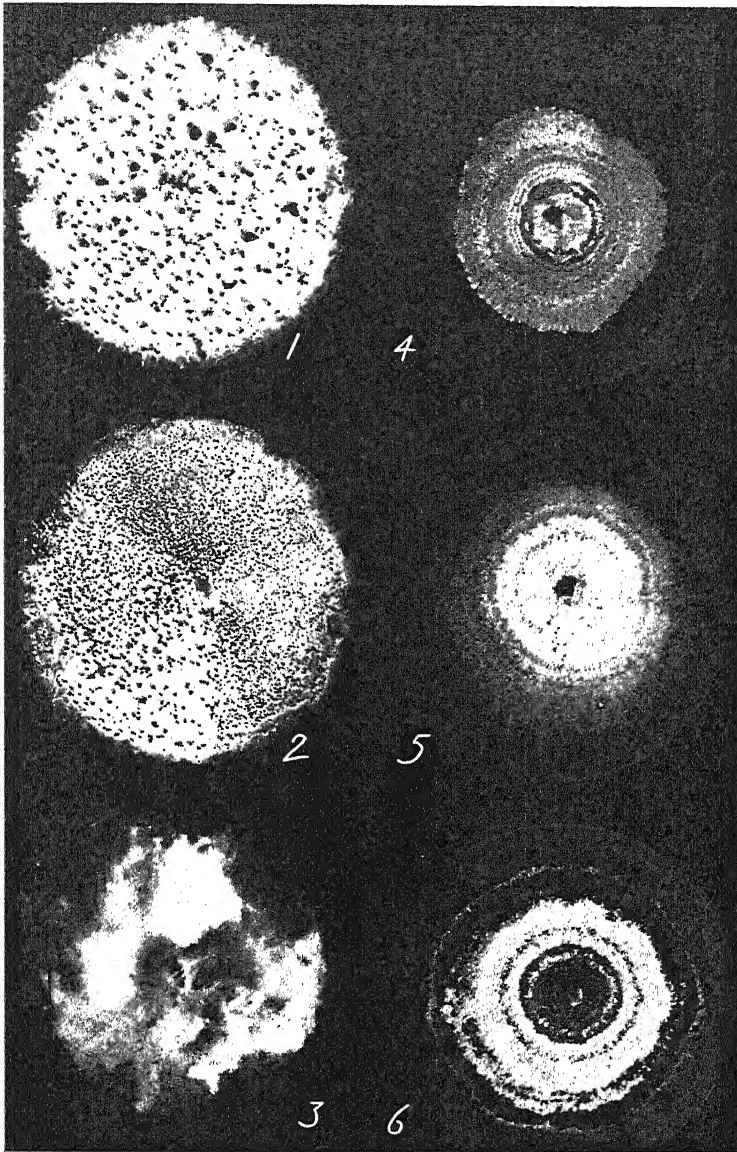
Fig. 1. Six races of *Pestalozzia funerea* isolated from pine needles. Cultures grown under similar conditions. *1*, race 8; *2*, race 2; *3*, race 7; *4*, race 3; *5*, race 6; *6*, race 4.

SPORE PRODUCTION

In the comparative study of these races on the three different media, the number of days elapsing from the time of inoculation of the flasks to the appearance of acervuli in each culture was recorded. While it is recognized that this is a character which apparently may vary somewhat with slight changes in environment, yet in a strictly comparative study, carried out under conditions which permitted only very small differences in environment between any two cultures, great differences in the time, manner, and abundance of spore production may be assumed to carry some weight in the differentiation of races, especially when coupled with other characteristics.

Wenner (1914), working with *Pestalozzia funerea*, found that his original cultures formed conidia in ten to fifteen days after inoculation, while his later cultures, which were subcultures of the original ones, formed conidia in three days. He said that possibly the fungus had become better adapted to the medium. The evidence which has been collected against the theory of such rapid adaptation of fungi would make it seem possible that the phenomenon might be explained more plausibly in either of the following ways: Either he gradually and unconsciously changed the medium to suit the conditions necessary for the production of spores, which is unlikely, or, which seems more probable, he had a mixed culture of several races and gradually selected those which produced conidia in a short time. It is possible, too, that variants may have arisen which produced spores in a shorter time than the parent cultures. In the races studied by the writer great differences were found in the time required to form spores. One race produced an abundance of spores in three days, another required thirty days to produce spores, and some did not produce any at all. (See table 1). Repeated experiments have proved this to be a constant character.

Not only was there considerable difference in the time required to produce spores but there was also an appreciable difference in the abundance of acervuli produced, and in their size and position on the culture. For example, cultures of race 25 always produced an abundance of acervuli distributed over the surface of the culture in several broad, black bands, while in cultures of race 26 they were produced in fewer numbers and were distributed evenly over the surface. In cultures of race 18 they were produced in great abundance, evenly distributed over the surface, appearing as tiny, slightly protruding pimples, while in cultures of race 17 they were very sparsely produced, and appeared in isolated groups; they looked like specks of dust on the surface, so small that they were barely perceptible.

A biometrical study was made to determine whether there were significant differences in the size of spores of the different races, using only those races in which it was thought, from general observation, that differences might be present. The technique of obtaining a random sample was as follows: An inoculating needle was drawn across a culture several times, and the spores so obtained were placed in a test tube containing about 5 cc. of distilled water. The tube was thoroughly shaken and several drops of the spore suspension were placed on a slide. One hundred spores from each race were measured. The results are given in table 2. It is apparent that no important difference was found in the length of spores and length of median cells between any two of the races studied, but there is a distinct

TABLE 1

Number of days from inoculation to production of acervuli in seven races of Pestalozzia funerea grown in duplicate on three different agar media at room temperature.

RACE	MEDIUM					
	MALT		RICHARD'S		COON'S	
	FLASK		FLASK		FLASK	
	1	2	1	2	1	2
1	18	18	13	10	18	18
3	—	—	—	—	—	—[1]
5	3	3	3	3	3	3
24	30	33	18	24	17	17
10	13	13	17	17	12	12
8	8	8	6	6	6	6
21	4	4	4	4	4	4

[1] No acervuli formed.

difference in length of setae. In race 2–1 the setae averaged 15.63 microns in length, while in race 10–2 they averaged 33.93 microns, or more than twice as long. This difference is large enough and constant enough to separate these two forms rather sharply. The other forms were intermediate between these two.

Guba (1929) has made a key for a part of the genus *Pestalozzia*, in which he separates the different species largely upon the basis of spore measurements, the length of median cells of *P. funerea* being from 15 to 18 microns. Two of the races studied by the writer fell below the lower limit, and the other two were just above it. Guba gives the upper limit of length of setae in *P. funerea* as 20 microns, but the foregoing analysis shows that some may exceed this limit by more than ten microns. These apparent discrepancies between Guba's results and the writer's may be

due to the fact that the spores measured by Guba were obtained from plant tissues, while those measured by the writer were from cultures on an artificial medium, although it is possible that some of the races investigated by the writer were genotypically different from those with which Guba worked. Or, it may be a combination of both heredity and environment. Whatever the true explanation may be, it would seem desirable to widen the limits of the species somewhat.

It is not the aim of the writer to set up a criterion whereby the different races of this fungus might be differentiated from one another on the basis of morphological differences in the spores; even if that could be done, it would be of little advantage. It is desired to show merely that there are

TABLE 2

Comparison of length of spores, length of three median cells, and length of setae of different races of Pestalozzia funerea.

Race	17–1	21	10–2		
Length of spores	23.768	22.248	22.851		
Probable error	0.125	0.105	0.111		
Race	17–1	10–2	12	2–1	
Length of median cells	15.069	15.276	14.409	14.313	
Probable error	0.073	0.060	0.067	0.060	
Race	21	10–2	12	2–1	5
Length of setae	18.42	33.93	16.53	15.63	24.96
Probable error	0.206	.391	0.379	0.233	0.305

perceptible differences between the spores produced by the different races when grown under similar conditions. The data are given as added proof of the existence of distinct races within the species.

Coloring of the median cells also has been considered an aid in separating species of *Pestalozzia*. In the different races studied by the writer the cell coloring varied sufficiently to serve as a distinguishing characteristic of certain races. For example, numbering the three colored cells consecutively from the end which bears the stalk toward the end which bears the setae, the following differences were observed. In the spores of race 21 the first colored cell was light brown, and the second and third were very dark brown. In the spores of race 2 the first colored cell was almost transparent and the other two were very light brown, being about the same color as the first cell in the spores of race 21. In the spores of race 12 the first colored cell was almost transparent, the second was dark, and the third was slightly lighter than the second. Races 21 and 2 could be separated from each other and all others on this basis, and race 12 could be separated from

some of the other races, but not from all, on the same basis. These differences within one species make it seem likely that coloring of the median cells may not always be a very reliable character for delimiting species.

These dissimilarities in the spores were not dependent upon the age of the cultures. In so far as the writer has been able to determine by general observation and biometrical study, there is no perceptible variation in the
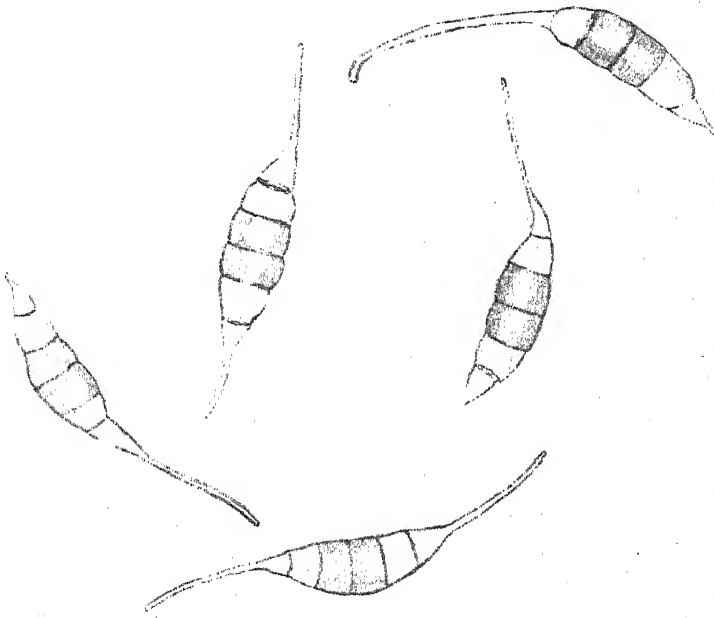
Fig. 2. Spores of race 4. Each spore has only one seta. Drawn with the aid of a camera lucida.

size, shape, or color of the spores, length of setae, or length of basal appendage with increasing age of the culture. This confirms the observations of LaRue (1922) in his biometric study of *P. Guepini*, where he found that there was no measurable difference between the spores produced early in the life of the culture and those produced later.

With two exceptions, in every race of *P. funerea* in which spores were produced the spores were five-celled. Race 4, which did not produce spores on ordinary media, was grown on tube slants of malt agar to which had been added several pieces of longleaf pine needles, after the medium was

tubed but before it was sterilized. In this medium the fungus grew more rapidly than on the malt agar alone, and after two weeks it produced several acervuli. The spores had only one seta. Several of these spores were drawn with the aid of a camera lucida and are shown in figure 2. Race 3, which resembled race 4 somewhat in cultural characters, and, like it, did not produce spores on standard media, produced spores on malt agar to which had been added a trace of benzaldehyde, and it produced a few acervuli on malt agar to which had been added a trace of ethylene chlorhydrin. These spores were nearly hyaline, and, like those produced by race 4, had only one seta. Race 6 resembled races 3 and 4 in culture, but on malt agar it produced a few spores, which were not borne in acervuli but were scattered singly over the surface of the cultures. Some of them had five cells, some had six cells, but all had only one seta.

Saccardo (1907) distinguishes the genus *Pestalozzia* from the genus *Monochaetia* on the basis of number of setae—*Monochaetia* having only one and *Pestalozzia* having two to six. The cultures described above, which produced spores with one seta, were derived from single spores, which in turn were obtained from the same acervulus as were other spores which gave rise to races that produced spores with three setae. It is not likely that two genera of fungi would be fruiting in the same acervulus. Nor is it likely that *Monochaetia* spores would, by chance, so frequently lodge on an acervulus of *Pestalozzia*. It would seem more probable that these spores with one seta are just another variation within the species and that the old classification is not an entirely dependable one. Further proof of this statement is given later.

THE PRODUCTION OF VARIANTS

Triangular sectors, usually originating at the center of the colony and continuing out to the edge, appeared in some of the monosporous cultures. The sectors in the cultures were distinguished in various ways from the parents from which they originated: some were characterized by increased production of acervuli, some by decreased production; or the distribution of acervuli was different, the parent producing them in clear cut concentric bands and the sector producing them evenly over the surface; or the parent produced a multitude of tiny acervuli and the sector produced only a few large, prominent ones; or, as happened more often, the sector appeared to have lost the ability to produce spores in culture. Some of the sectors were distinguished by mycelial characteristics. A few of the sectors will be described.

In culture 1 of race 12 a very clear cut sector was formed in which few acervuli were produced until several weeks after acervuli had been formed

in the parent culture. In the parent culture acervuli developed so profusely as to literally blacken the surface. This parent culture and the mutant from it were carried through six generations in duplicate on malt agar and on Richard's agar. The parent culture consistently produced an abundance
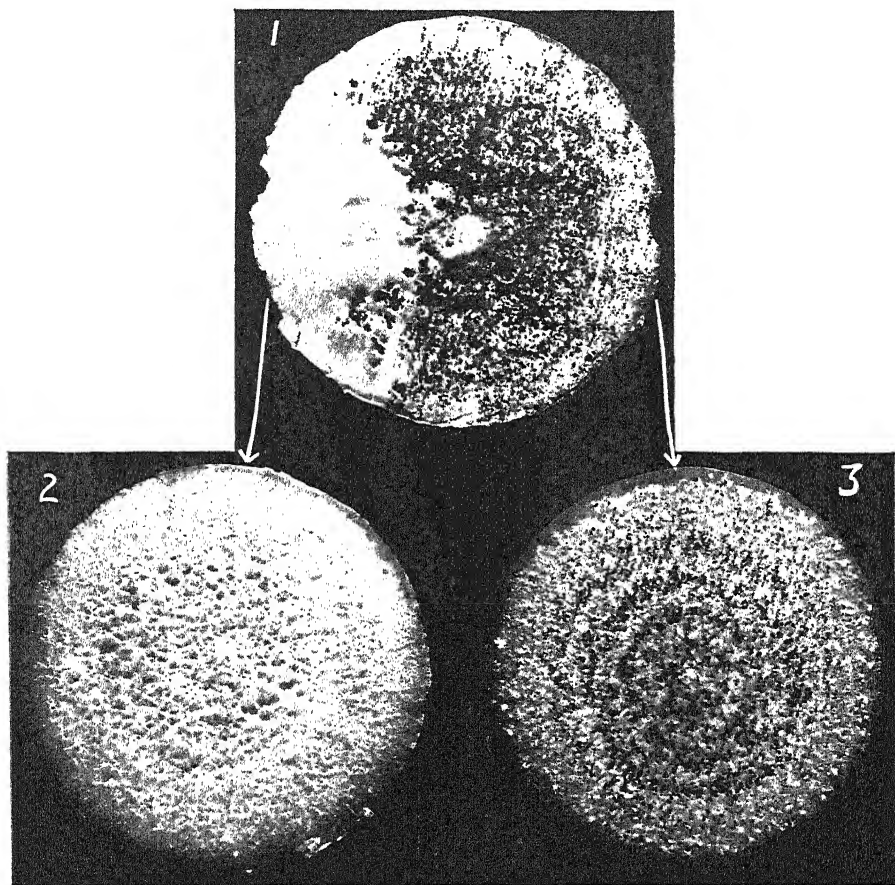
Fig. 3. *1*. A culture of race 12, on Richard's agar, showing a sector in which no spores are produced. *2*. A subculture from the sector. *3*. A subculture from the sporulating area. *2* and *3* are of equal age, grown on malt agar.

of acervuli within a week after being transferred, while the sector just as consistently failed to produce any acervuli for over three weeks after being transferred, and produced only relatively few after that. This parent culture and the subcultures from it are shown in figure 3.

Culture 1 of race 10 formed a sector which produced no acervuli, although the parent fruited abundantly. The parent and the sector were

grown side by side in duplicate flasks on malt, Richard's and Coon's agar, and the parent always produced numerous acervuli, while the cultures from the sector just as consistently failed to produce any.

Also, different strains suddenly arose in some cultures without manifesting their presence in any visible way. Inoculum from different parts of a culture which was to all appearances perfectly homogeneous in character resulted, in several instances, in subcultures which differed greatly in certain characteristics of growth. Such a difference appeared in one of the cultures of race 1 on malt agar. This culture had been grown for over five months, through several transfer generations, and up to this time had appeared to be a constant race. One of its characteristics had been the production of a large number of acervuli, from which the spores were exuded in a long, coiled tendrils. When transferred later for the purpose of making a comparative study, all the subcultures of this form on the different media produced only very few acervuli. In addition, the duplicate cultures on malt agar differed considerably from each other. In one the mycelium was white, abundant, slightly flocculent, and had several indistinct concentric rings. In the other the mycelium was less abundant, more appressed, had only one concentric ring, and was colored a light yellow. The agar was colored also by the yellow mycelium which grew through it. The yellow color was diffused and collected in granules throughout the protoplasm of the hyphae. This yellow variant has been grown on malt agar for five generations and on three other media for one generation, and it has constantly produced the distinctive yellow color.

From the foregoing descriptions of several of the cultures it can be seen that some races of this fungus are rather unstable even under ordinary cultural conditions. Other races, on the contrary, have been carried through numerous transfer generations for more than twelve months without displaying any visible inconstancy. Certainly not all of the variants which appeared in sectors and otherwise have been continued in culture long enough to enable one to state positively that their characteristics are constant. However, a number of them have been grown for more than a year on several different kinds of media, and during this time they have made no further permanent changes (excepting those in which sectors were formed) and the final cultures were exactly like the originals. Nor have any of the variants reverted to the parent types. From this it is only reasonable to assume that the other sectors will continue with the same degree of constance, except in instances where divergent forms may appear suddenly.

Many of the variants which appeared were characterized by a partial or total loss of sporulating ability, but some of them, on the contrary,

showed a gain in the ability to produce spores, as is illustrated in figure 4. It is possible, also, that this apparent gain may have been due to the loss of some factor which previously had inhibited the formation of spores.

Race 21 gave rise to an unusual and exceedingly interesting series of variants. Cultures of this race always produced such great numbers of spores that the surface was blackened, and little mycelium was visible. It first produced a variant which differed chiefly in a greatly decreased sporulating ability, scattered acervuli being borne in the mycelium above
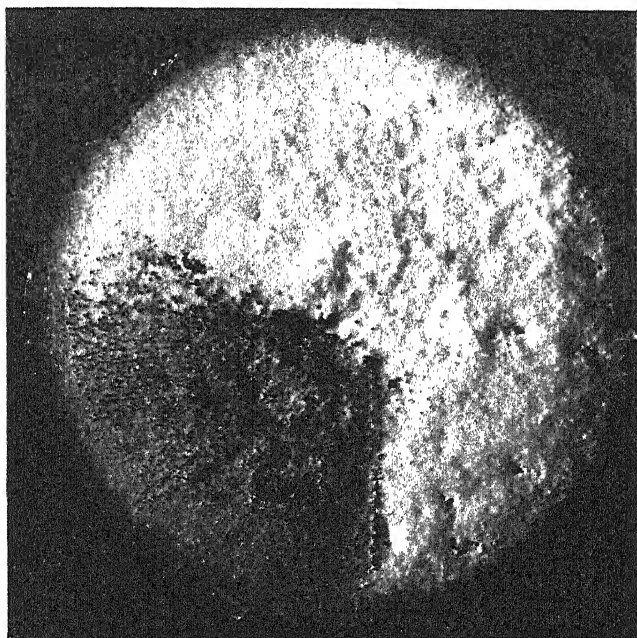
Fig. 4. Race 2–1, on malt agar, showing a sector in which the sporulating ability is increased.

the surface of the agar. After several months a sector appeared in one of the cultures of this variant. In the sector numerous acervuli were borne, considerably more than in the parent, and they were always formed beneath the surface of the agar. In the parent, out of 200 spores, 21 had 2 setae, 158 had 3 setae, 20 had 4 setae, and 1 had 5 setae. In the sector, out of 200 spores, 30 had 1 seta, 155 had 2 setae, and 15 had 3 setae. None was observed that had more than 3 setae. Ten of the spores having only 1 seta were isolated, and in the cultures resulting from these isolations by far the largest number of the spores had only 1 seta; about two out of every hundred had two setae, and none was found with more than two setae. Not all

of these spores with one seta were normal in size, shape, or color. The aberrant ones had from two to six cells, and ranged from hyaline to normal in color, and sometimes the seta arose from the side of the end cell, instead of from the tip, and occasionally a spore was found in which the seta arose from the side of one of the median cells. Also, some spores appeared to be without a seta. These cultures were grown on malt agar and on Coon's agar, media upon which the parent cultures grew and sporulated very readily, so that any change which occurred was more likely in the genetic makeup of the fungus, not a temporary variation due to environment. This variant has been grown on malt agar for approximately a year, and the characters appear to be constant.

Several spores with two setae were isolated from this sector also, and the cultures derived from these isolations produced spores with two setae almost exclusively, the setae being considerably longer than those of the parent. In these cultures there were few aberrant spores, no more than are found normally in any culture, and the spores were borne above the surface of the agar, as in the parent.

The above variant which produced spores with two setae gave rise to another variant race, distinguished in culture by a marked increase in spore production, producing even more spores than race 21. In this variant, out of 200 spores, 1 had 3 setae, 164 had 2 setae, and 35 had 1 seta. The spores with one seta could be distinguished easily from the spores with 1 seta produced by the variant previously described, because the setae were much longer, and all of the spores were normal in shape. Single spores with 3 setae, 2 setae, and 1 seta were isolated from cultures of this variant, and the cultures resulting from all of them were similar, and, in all of the cultures, spores with 3 setae, 2 setae, and 1 seta were produced in approximately the same ratio as those of the original cultures of the race, namely 164:1:35. Thus, the range of variability of the variant race is greater than that of the parent, and here the spores with 3 setae and with 1 seta are only expressions of the normal range of this particular race. To sum up this series of unusual variants, there have been obtained from an original race bearing spores with 3 to 5 setae:

(1) A race which produces spores each with a single, short seta.
(2) A race which produces spores each with two long setae.
(3) A race which produces spores with 3 setae, 2 setae, and 1 seta.

Fig. 5. A series of variant races produced by sectoring, the order of their origin being indicated by arrows. Race 21 is the original, isolated from the longleaf pine. 21-1 is a variant produced by 21. 21-1-1 and 21-1-2 arose simultaneously in 21-1. 21-1-2-1 is a variant produced by 21-1-2. 21-2 is a later variant of 21. All cultures three weeks old, grown on malt agar.
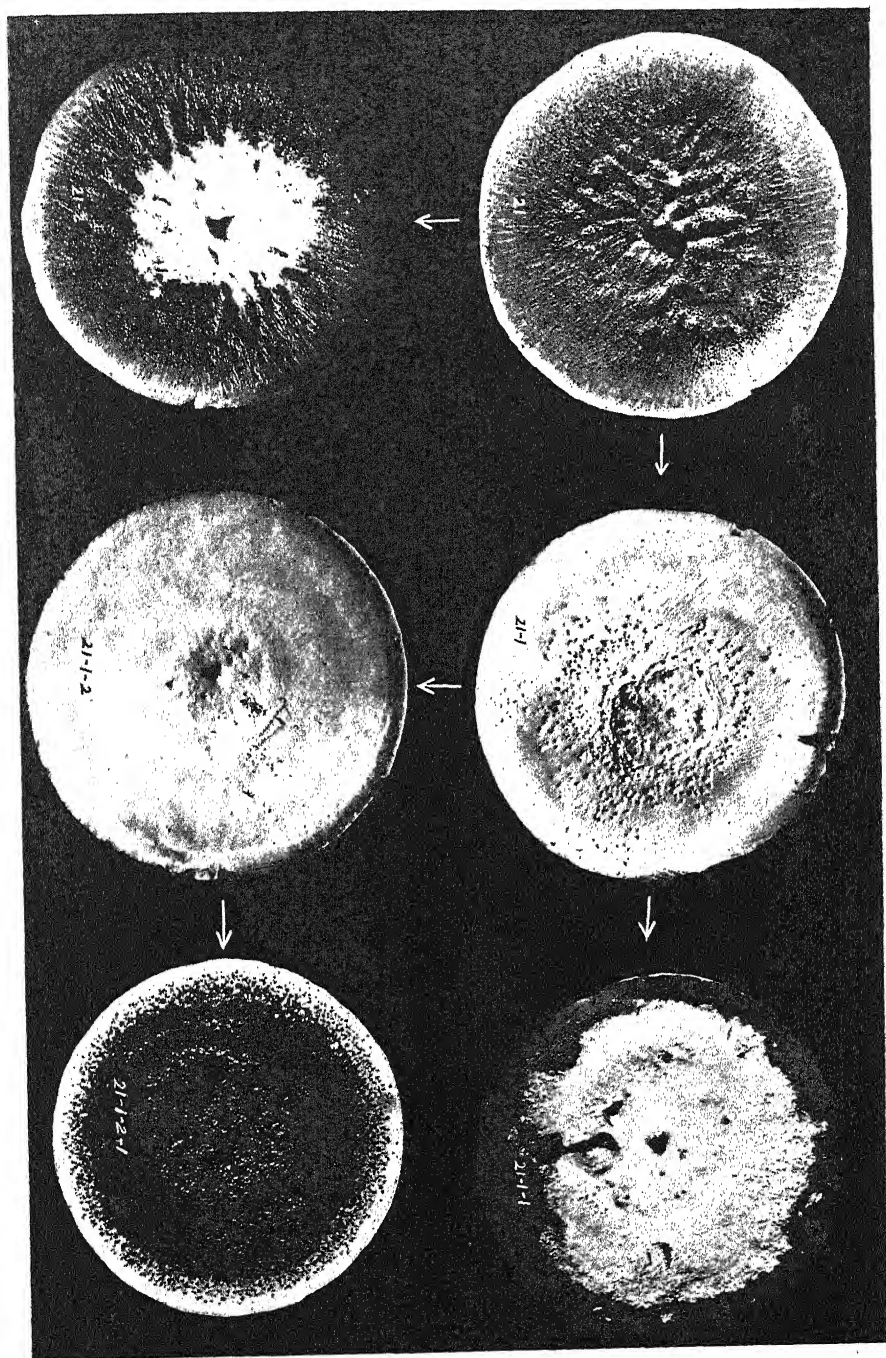
Fig. 5. See opposite page for explanation.

This series of variants and the spores produced by them are shown in figures 5 and 6.

The writer's experiments give little indication of the fundamental causes concerned in the origin of these new races. Results of staining show that some hyphal cells have one nucleus and some may have two, but it is not known whether this is significant in the origin of new races. The nuclear condition of the spores is not known. Until the facts are known in regard to the cytological phenomena associated with spore formation, spore germination, and the development of hyphae in these races, one can not state positively how these new races came into being.

The asexual condition of the fungus precludes the possibility of normal hybridization and segregation, at least immediately preceding the formation of sectors. It is possible, however, that sexual fusions occurred somewhere in the history of the fungus, and that the production of the present variants is the result of a very much delayed segregation of factors, although this assumption seems hardly credible. A heterokaryotic condition, originating in some previous sexual process, and continually becoming increased through hyphal fusions, could be responsible for the variants which have appeared. Or, as Brierley (1931) suggests, hyphal fusions in some of the Fungi Imperfecti may be sexual in nature. Either of the last two assumptions, if correct, would explain how a heterokaryotic condition might arise and continue, so that, instead of obtaining a pure line from a single spore, one might get a colony in which different hyphal cells would contain genetically unlike nuclei, or different combinations of unlike nuclei. The spores produced by these different hyphae would not be genetically alike, and the chance of isolating a genetically homogeneous race from such a colony, by isolating single spores, would be remote.

There is little reason to suppose that the origin of variants is limited to one single cause, and it may be that the variations in these races can not be adequately described unless all of the above assumptions, including mutation, be taken into consideration.

Certainly it would be somewhat illogical to assume that these relatively permanent changes in the organism were only adaptations to variable or abnormal environments, even though the environment may have been a

Fig. 6. Photomicrographs of spores of different races. Two upper pictures: Left, race 2; right, race 10, showing difference in length of setae. Four lower pictures: The numbers indicate the races (shown in Fig. 5) from which the spores were taken; the arrows indicate the order in which the variants appeared. Note the single, short seta on each spore of 21-1-1, the two long setae of each spore of 21-1-2, and the single long seta of two of the spores of 21-1-2-1. Races 21-1-1, 21-1-2, and 21-1-2-1 were photographed with a higher magnification than the others.
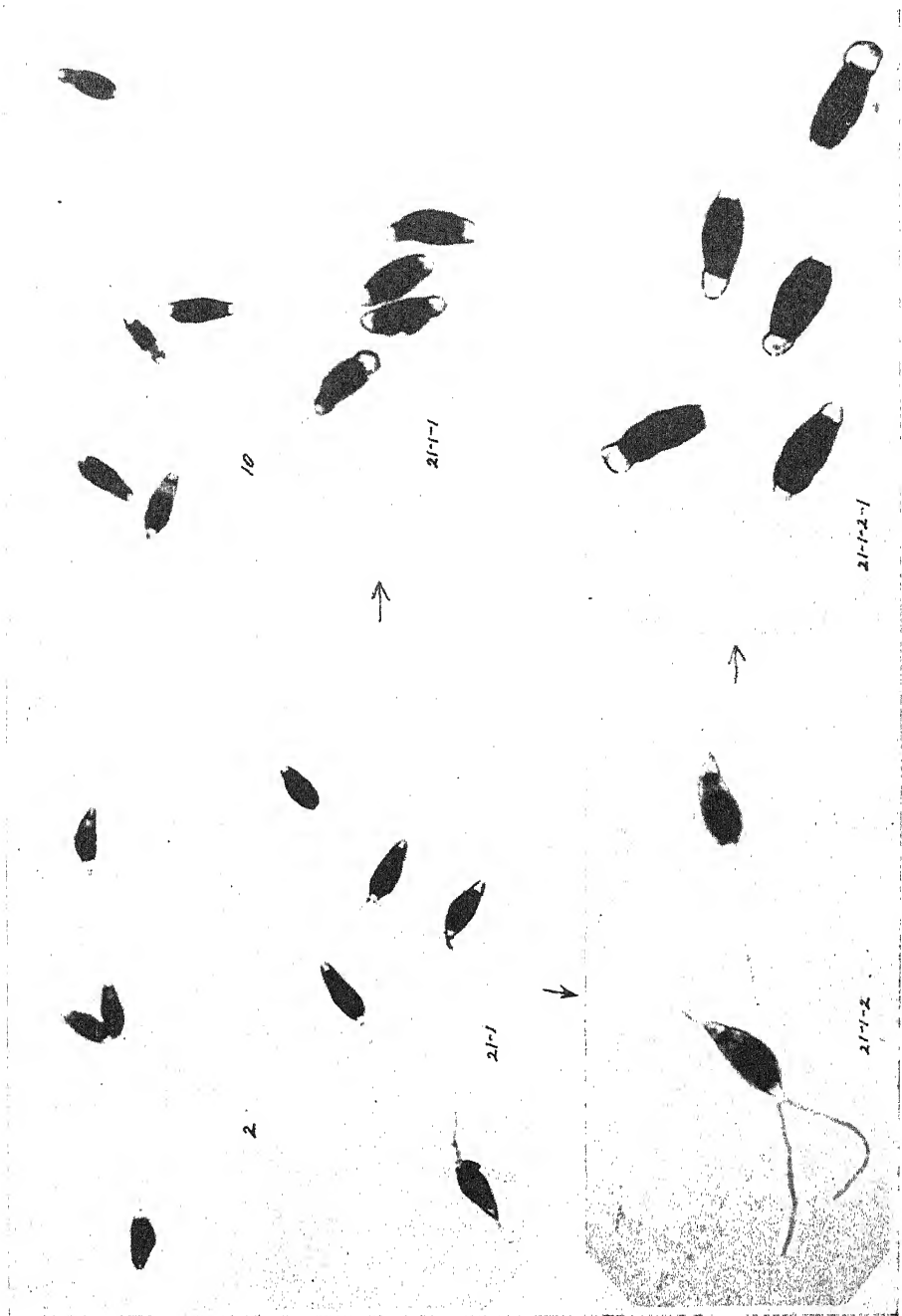
Fig. 6. See opposite page for explanation.

factor in the production of these variants. Races which arise fortuitously
at irregular intervals, and which retain their newly acquired characters,
hardly can be considered ordinary, temporary modifications. Especially is
this true of variants showing new morphological characters, of which the
race bearing spores with only one seta is a striking example.

The origin of a variant differing so much from the parent in morpho-
logical characteristics that it could be placed in a different genus, seems
significant. There are two possible explanations of this: either the new race
is a previously undescribed variant of *Pestalozzia funerea*, and the limits of
the species must be widened accordingly, and the genus *Monochaetia* con-
sidered no longer valid, or else the author has observed the birth of a
species of *Monochaetia* from a species of *Pestalozzia*. The race bearing
spores with two setae, and the race bearing spores with one, two, and three
setae are evidence in favor of the former interpretation.

The evidence presented proves that new races of *P. funerea* have arisen
in culture, differing from their parents either physiologically, or mor-
phologically, or both. These new forms have retained their characters,
except when they again produced variants. Although the mechanism of
their origin is not known, mutation, in the sense in which Baur (1922) and
Stakman et al (1929) used the term, would seem to explain the process
more exactly than any other. An academic discussion of the appropriate-
ness or correctness of the several terms which different investigators have
applied to similar phenomena in other fungi is hardly within the province
of this paper. Thorough discussions of the subject, illustrating the different
points of view concerning the occurrence of mutation and saltation in
fungi, are given by Brierley (1922), Brown (1926), and Stakman et al
(1929). But whether the described changes, both physiological and mor-
phological, be called by one name or another, is not so significant taxo-
nomically as is the fact that these changes occur. The essential fact for
taxonomists is that *P. funerea* has a wider range of variability than has
been ascribed to it in the past, that it consists of a number of races, and
that new races are continually being formed.

PATHOGENICITY

There is considerable conflict of opinion in the available literature in
regard to the pathogenicity of *Pestalozzia funerea*. Some workers have
found it to be a saprophyte, while other investigators, studying its patho-
genicity on the same and closely related species of trees, have found it to
be a parasite of some economic importance.

Spaulding (1907) published a report of a damaging needle blight of
Pinus ponderosa and *Pinus divaricata* caused by *P. funerea*. He inoculated

one-month-old seedlings of *Pinus ponderosa* and the disease was produced. Infection failed to appear on the one-year-old stock which he inoculated. Hartley (1913) isolated *P. funerea* from diseased jack pine and Rocky Mountain pine. He inoculated one-year-old white pine seedlings with spores obtained from these cultures, but no infection appeared.

Wenner (1914) found two parasitic forms, which have been discussed previously in this paper. One form was isolated by Prof. Graves from the stems of a badly diseased *P. Strobus* near New Haven, Connecticut. Other fungi were present in the diseased tissues. The second form was isolated by Wenner from the leaves of a five-year-old *P. Strobus* which had been kept in the greenhouse for several months. He inoculated several different species of conifers with the spores produced in cultures. Infection resulted on one-month-old, one-year-old, and three-year-old white pine, one-month-old and two-year-old Norway spruce, and on one-year-old hemlock.

Graves (1914) reported a twig blight of Norway spruce which he states may have been caused by *Pestalozzia funerea*. Fischer (1912) found *P. funerea* parasitic in the leaves of *Pinus canariensis*, *P. longifolia*, *P. insignia*, *P. Massoniana*, *Cupressus lusitanica*, and *C. Lawsoniana*, and *Casuarina leptoclada*. Guba (1929) states that *Pestalozzia funerea* is restricted to plants of the family Pinaceae.

Thus it can be seen that there are divergent opinions upon the relation of this fungus to its host plants. To ascertain the role which this fungus played in the blighting of longleaf pine needles and to find out if it were capable of parasitising other species of pines several inoculation experiments were made. Seven different species of conifers were used. The seedlings were grown in the greenhouse and were from four to six weeks old when inoculated. About 200 Douglas fir (*Pseudotsuga taxifolia* Brit.) seedlings, and 100 each of white pine (*P. Strobus* L.), Norway pine (*P. resinosa* Ait.), and jack pine (*P. Banksiana* Lamb.), and 80 longleaf pine (*P. palustris* Mill.) seedlings were placed in inoculating chambers in the greenhouse and inoculated with *Pestalozzia funerea*. Spores from all the spore-producing forms of the fungus were taken from the cultures, suspended in distilled water and sprayed onto the leaves with an atomizer. The plants were left in the inoculating chambers for four days, then taken out and set on benches in the greenhouse. No infection appeared. The experiment was repeated with an equal number of trees of each of the species first used plus six slash pine (*P. caribaea* Morelet) seedlings about eight inches high, and about 150 Engelmann spruce (*Picea Engelmanni* (Parry) Engelm.) which had been grown in the greenhouse and were about two weeks old. Here also no infection resulted. From this it seems likely that those races of the fungus investigated by the writer are saprophytic and en-

ter the pine needles only after they have been injured by some other cause. This opinion would be borne out by the fact that *Pestalozzia* was found by the writer only on those needles of longleaf pine which had already been invaded and partially killed by *Septoria*.

<div align="center">CONCLUSIONS</div>

Pestalozzia funerea comprises many races or physiologic forms. This statement is attested to not only by the results of the writer's cultural studies of the fungus, but also by the lack of agreement in the results of other investigators who have studied the pathogenic capabilities and cultural characteristics of the organism. All the races described in this paper were isolated directly from two longleaf pine seedlings collected in Louisiana, or appeared as variants in these cultures. If more material, from other parts of the country or from other parts of the world, were collected, it is probable that more strains would be found. Not all of the forms which were discovered have been studied long enough to prove their existence as separate entities within the species, but the characteristics of a number of them have been established beyond all doubt.

The appearance of distinct and apparently permanent variants in some of these races has been observed but the mechanism by which they arose can not be known until more is known about the cytological phenomena involved.

The appearance of a sector which produced spores with only one seta may be of considerable mycological significance. The validity of the writer's previous inclusion in the species of forms which produced spores with one seta and five to six cells may have met with considerable doubt and some incredulity on the part of those who would have a place for everything and everything in its place, but, since these spores with only one seta were isolated from the host tissue and also obtained as a result of sectoring in cultures having spores with three setae, there is not much doubt that *Pestalozzia* occasionally does give rise to such forms. This should serve to clarify slightly the haze of uncertainty with which this group of fungi is surrounded. It seems to the writer that *P. funerea* is rather unstable, and, if this be true, it is far better to admit the fact, distressing though it may be, than to force rigid limitations upon a labile organism. If we are to adjust our conceptions to fit these new facts we must either widen the limits of *Pestalozzia* sufficiently to admit these new forms, and consider the genus *Monochaetia* invalid, or else concede that occasionally a species of *Pestalozzia* may give rise to a species of *Monochaetia*.

Pestalozzia funerea occasionally has been reported pathogenic upon different species of coniferous trees throughout the world. The writer's

inoculations of white, Norway, jack, longleaf, and slash pines, Douglas fir, and Engelmann spruce did not result in infection. From this it may be concluded either that the fungus is parasitic only under certain conditions, which were not maintained in these experiments, or that there are some strains within the species which are parasitic and others which are saprophytic.

<div align="center">SUMMARY</div>

1. Fifteen cultural races of *Pestalozzia funerea* were obtained by isolating 150 conidia from needles of longleaf pine. These races were distinguished from one another on culture media by the following characteristics: rate of growth, abundance, color, topography, and zonation of the surface and aerial mycelium, abundance, distribution, and size of acervuli, size, color and shape of spores, length of setae, and number of setae.

2. About ten distinct variants arose in the form of sectors in the above races and were distinguished from the parents and from each other by the characteristics listed under (1).

3. Three races obtained from spores produced in pustules on the needles of longleaf pine, and two races obtained from sectors in culture, conformed to the description given for *Monochaetia*, thus showing that our previous conception of this genus is scarcely tenable.

4. Seven species of conifers were inoculated with spores of different races of the fungus. None of the races were parasitic under the conditions maintained in the experiments.

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INDEX TO AMERICAN BOTANICAL LITERATURE
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